Why study an exotic animal?
Or what can we learn from barn owls about neuroscience?

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Which model system?

Animals that lend themselves to combined behavioral and neurophysiological work.

Specialist or Generalist?


120 ACA

Roger Payne

Mark Konishi
1933-2020

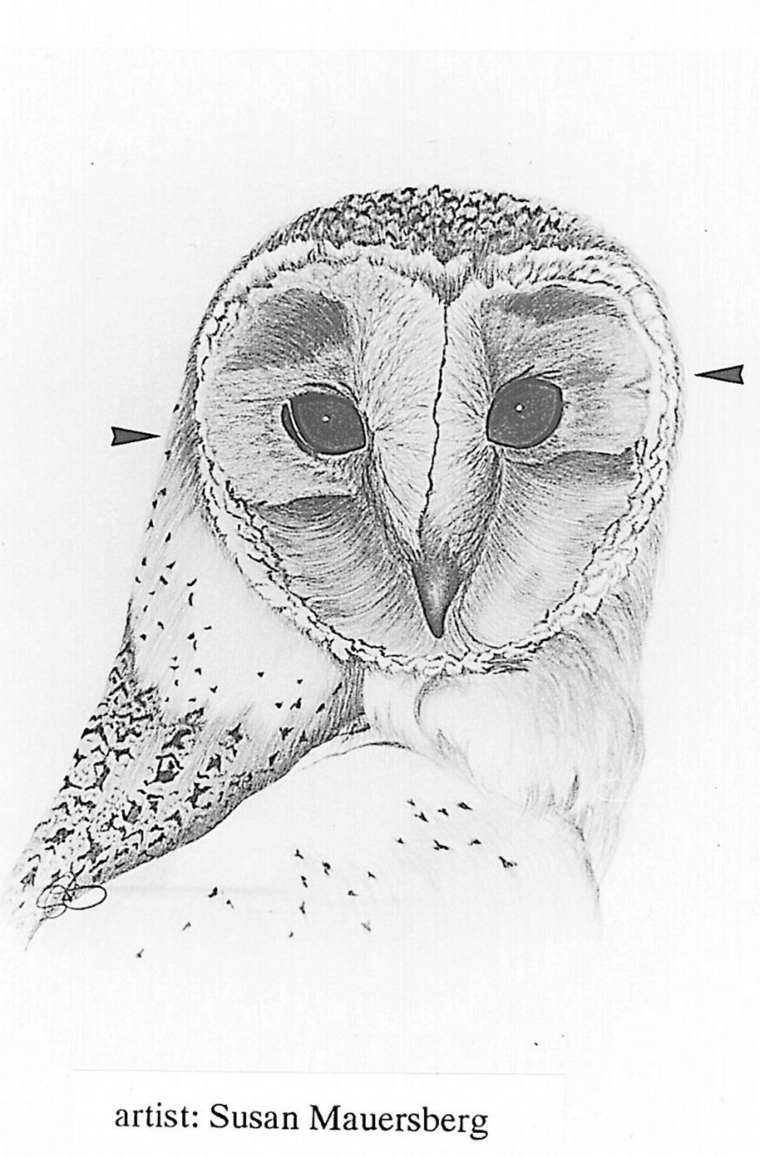
- **Sound localization**
- **Sensory maps plasticity and development**
- **Multisensory integration**
- **Selective attention**
- **Spatial representation in the hippocampus**

Barn owls as model system for sound localization

- Facial ruff serves as a sound amplifier

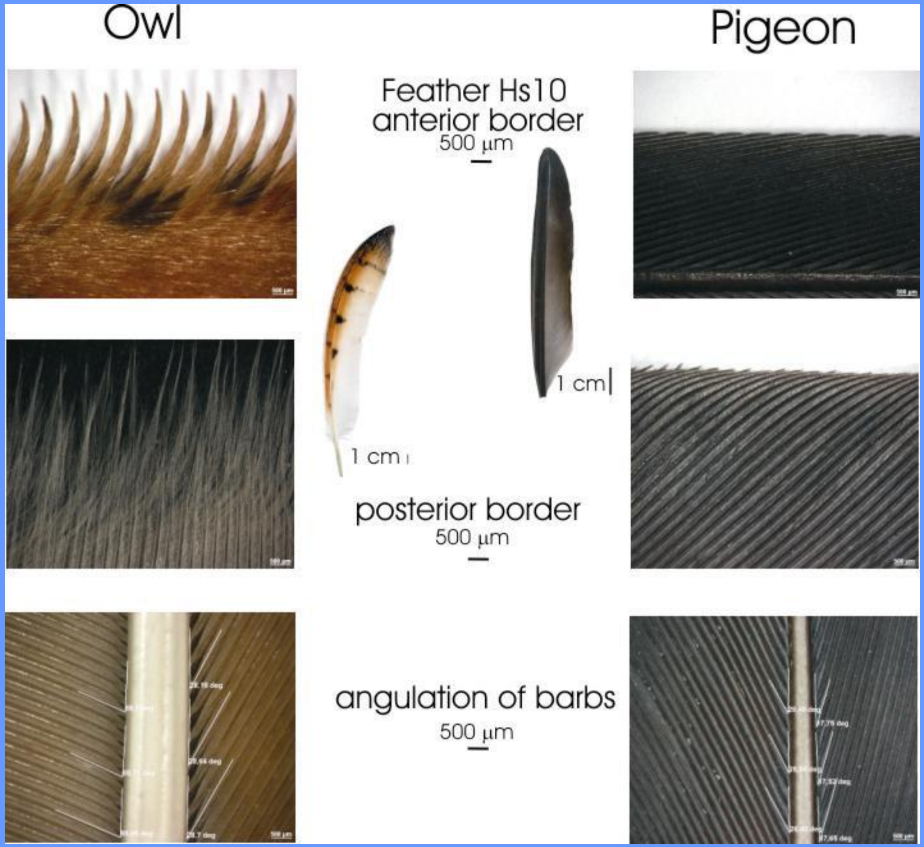
Barn owls as model system for sound localization

- Facial ruff serves as a sound amplifier
- Asymmetric ears allow for an increased spatial resolution in the vertical plane



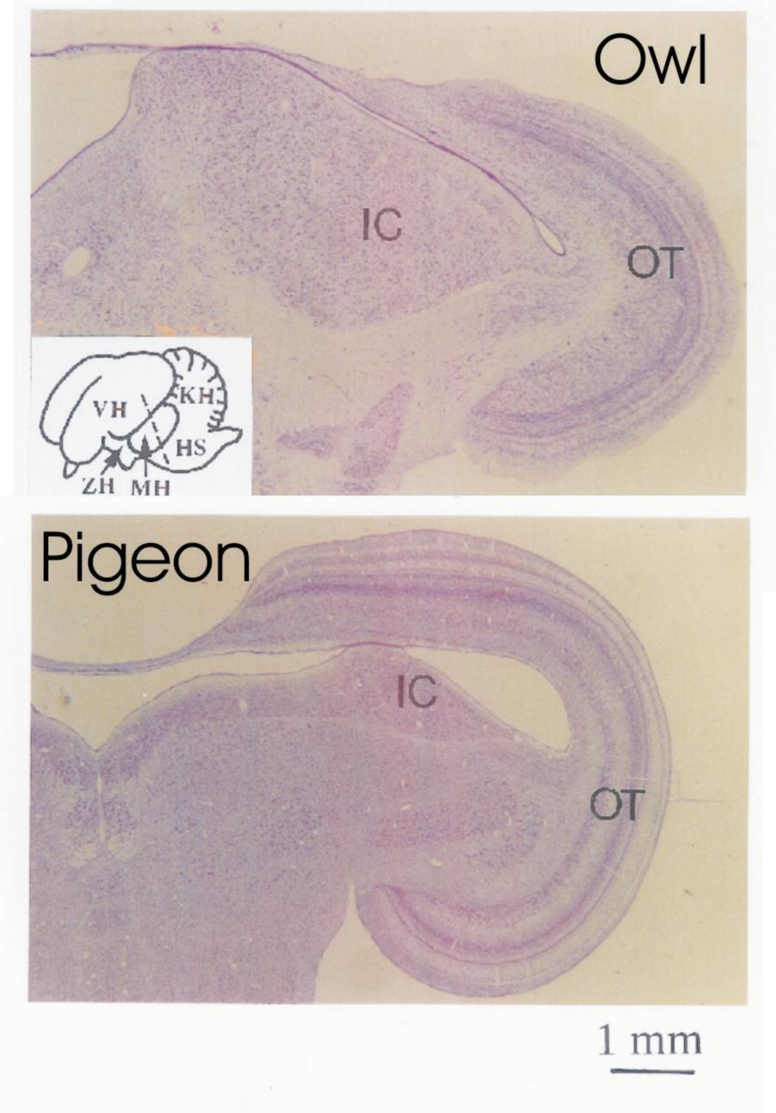
Barn owls as model system for sound localization

- Facial ruff serves as a sound amplifier
- Asymmetric ears allow for an increased spatial resolution in the vertical plane
- Comb-like structures at the leading edge of the wing reduce noise during flight

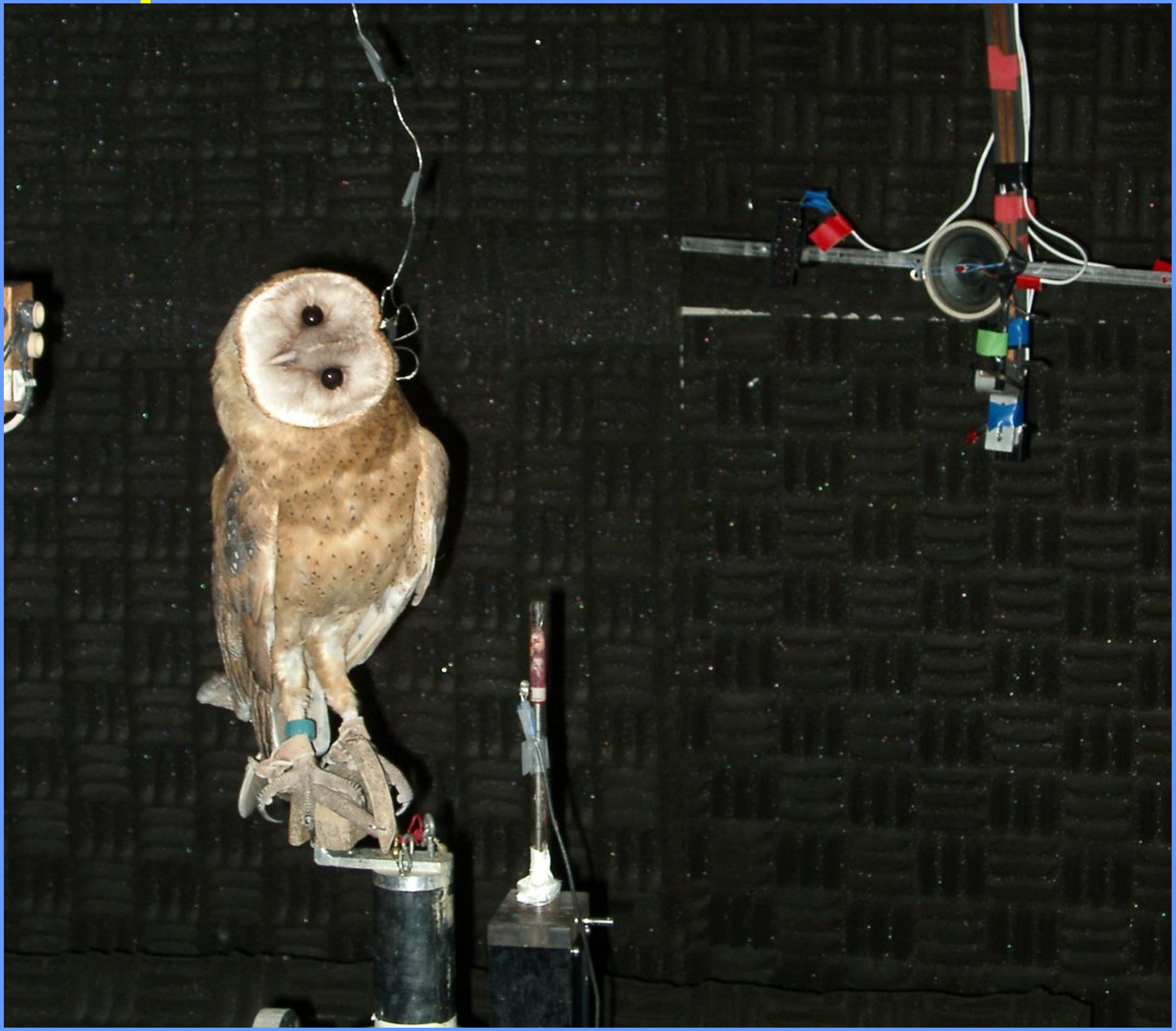


Barn owls as model system for sound localization

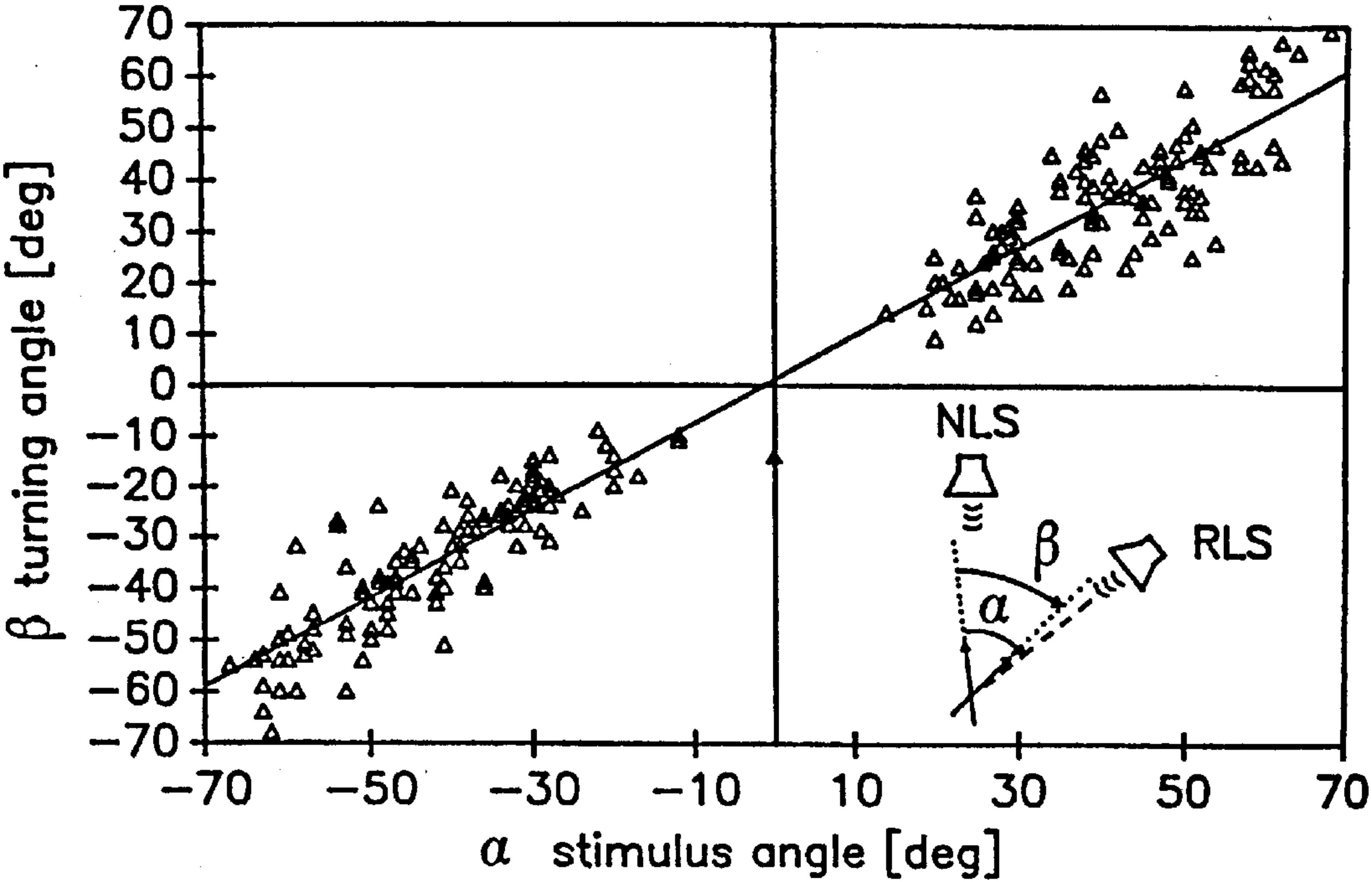
- Facial ruff serves as a sound amplifier
- Asymmetric ears allow for an increased spatial resolution in the vertical plane
- Comb-like structures at the leading edge of the wing reduce noise during flight
- Brain structures involved in the analysis of sound are enlarged



Performing a psychoacoustic experiment with an owl



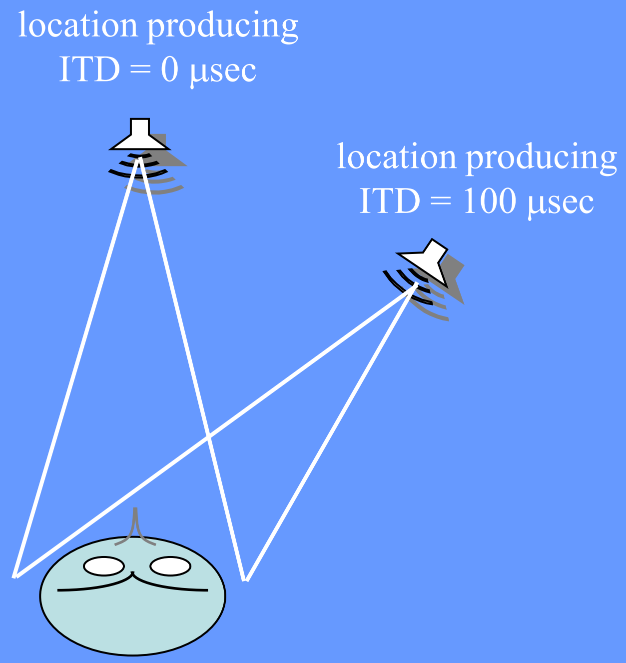
Sound-localization with free-field stimuli

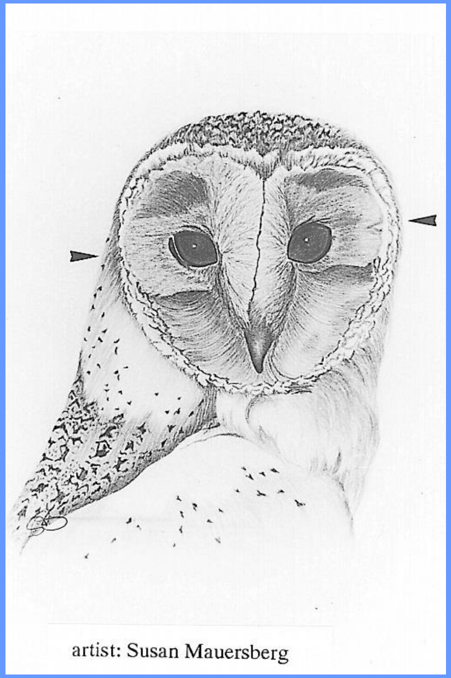


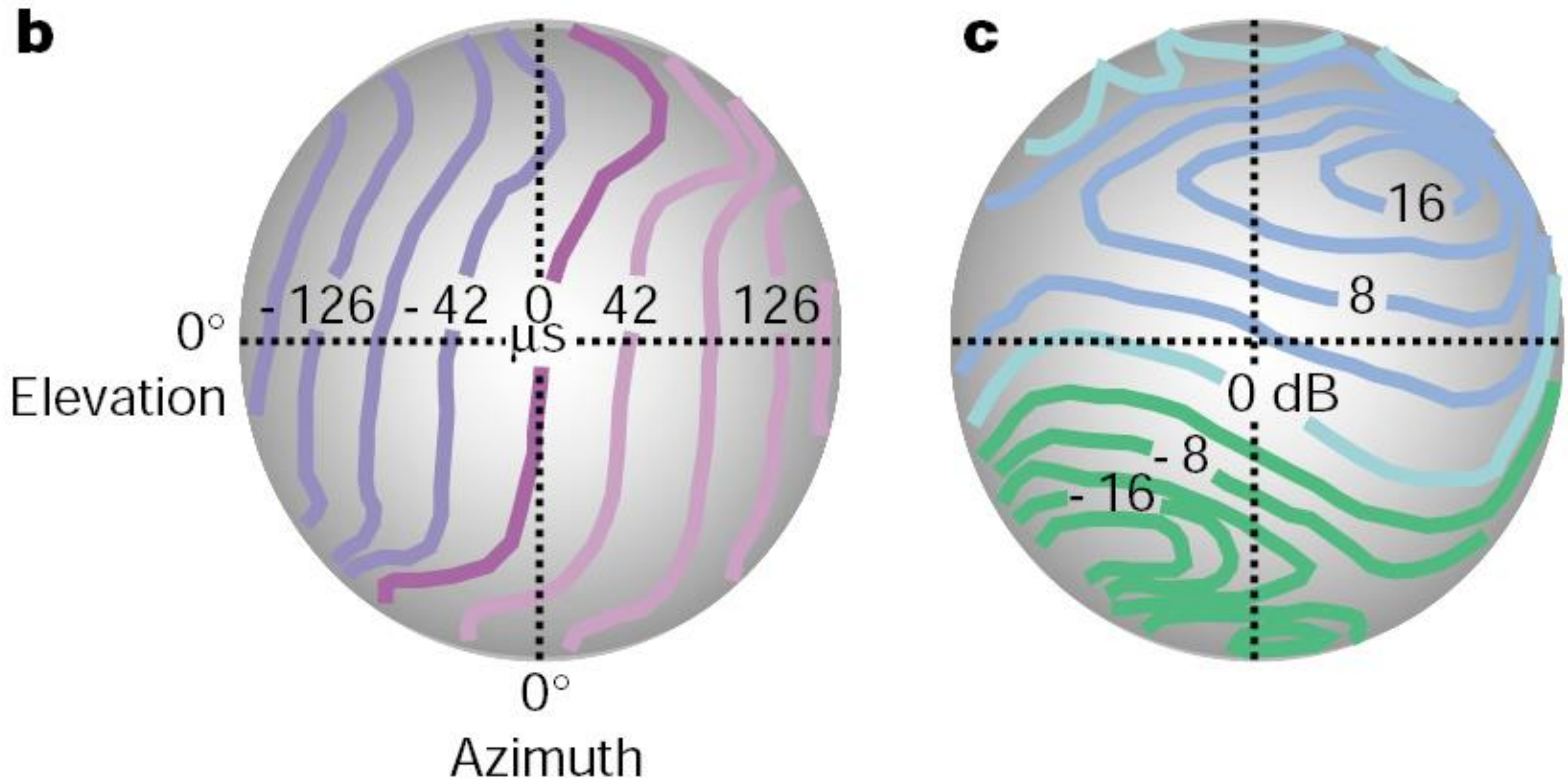
- The auditory localization cues:

- ITD - horizontal

ILD - vertical



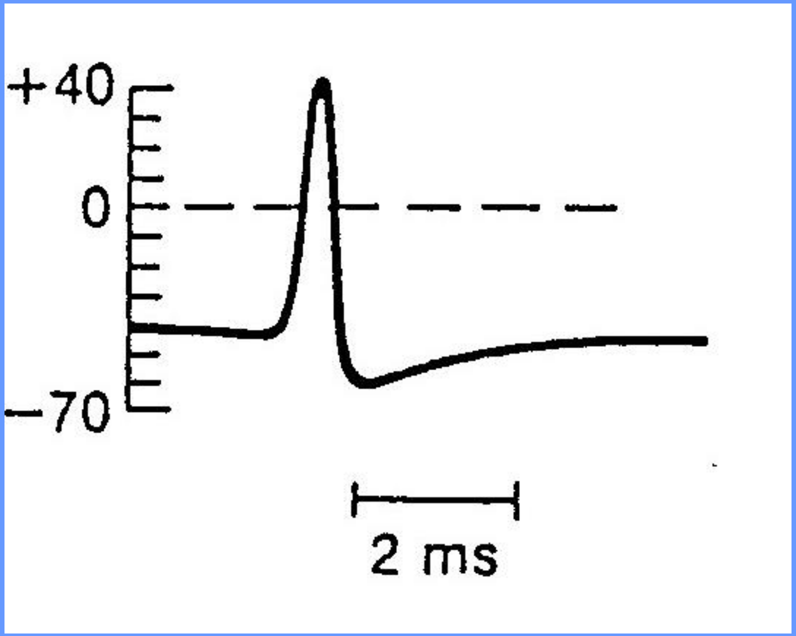


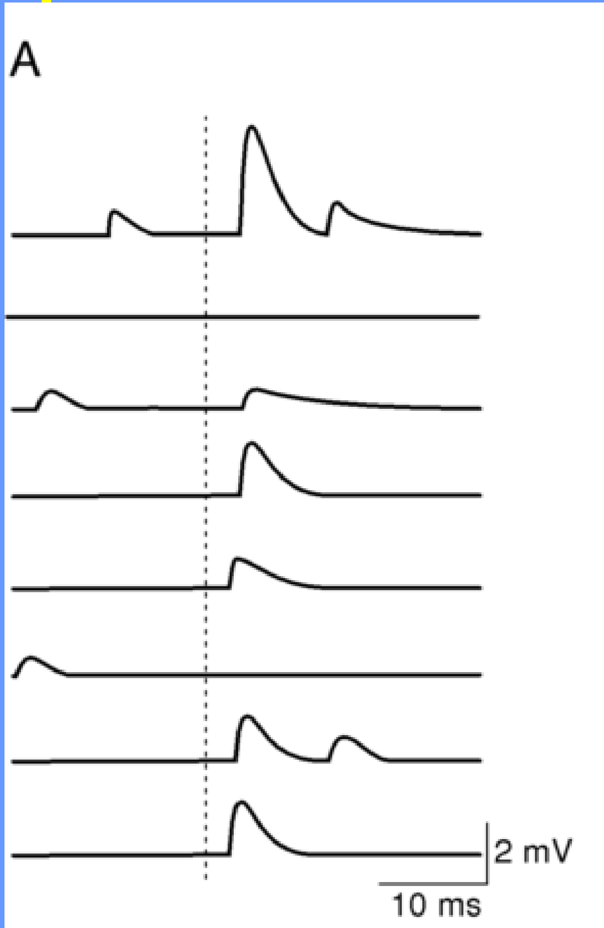

b
-126
-42
0
42
126
µs
0°
Elevation
0°
Azimuth
c
16
8
0 dB
-8
-16

Precision of sound localization in barn owls may be as good as 3 deg which corresponds to 6-10 μs.

Action potential

Postsynaptic potentials





These signals are the “language" of neural processing.

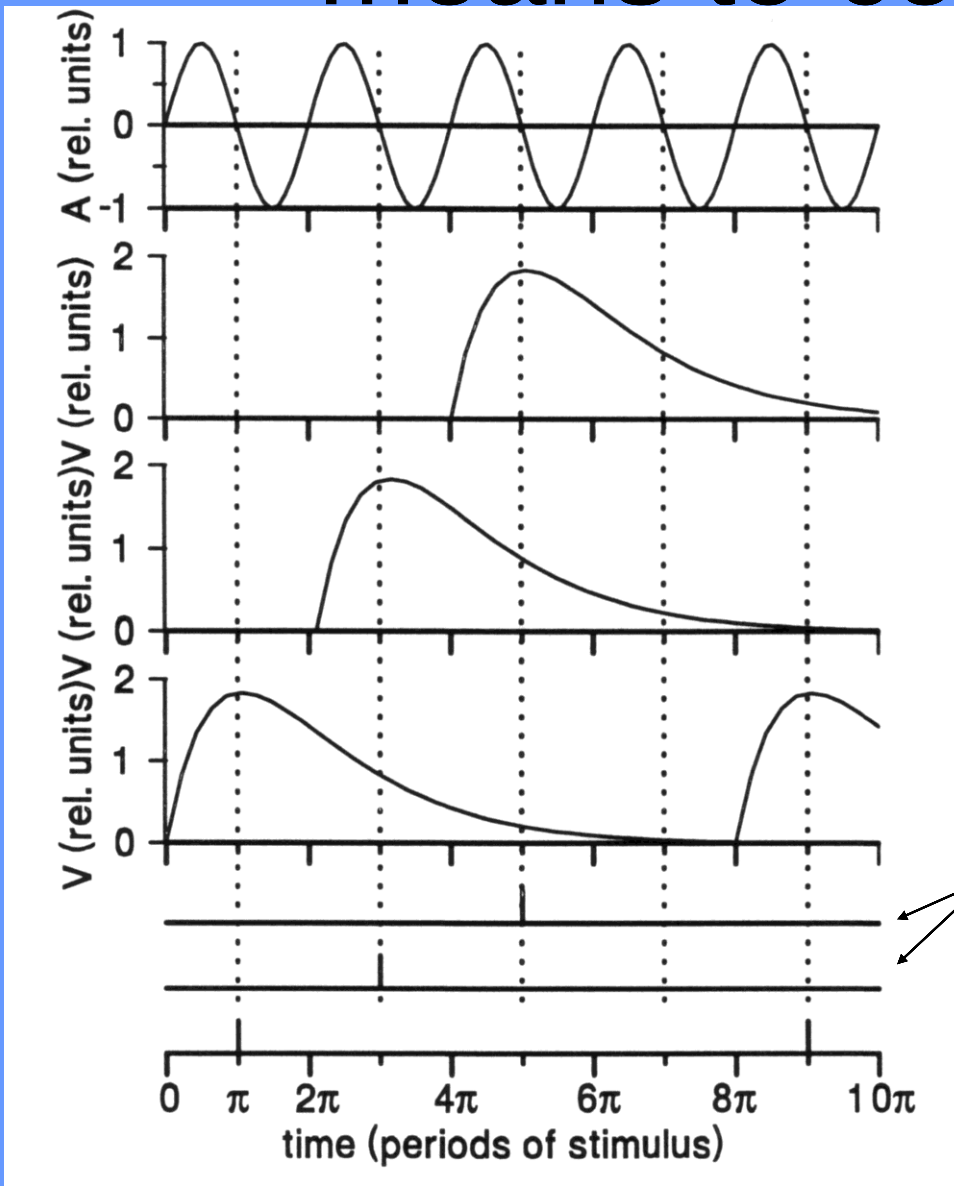
Durations of events

- Typical duration of action potential: 1ms
- Typical duration of
  post-synaptic potentials: 5-10 ms
- Precision of sound localization by
  interaural time difference: 6-10 μs

What has to be explained is

Factor of 500-1000

The principle of phase locking as a means to conserve time



Sinusoidal signal

Presumed resulting post-synaptic potential

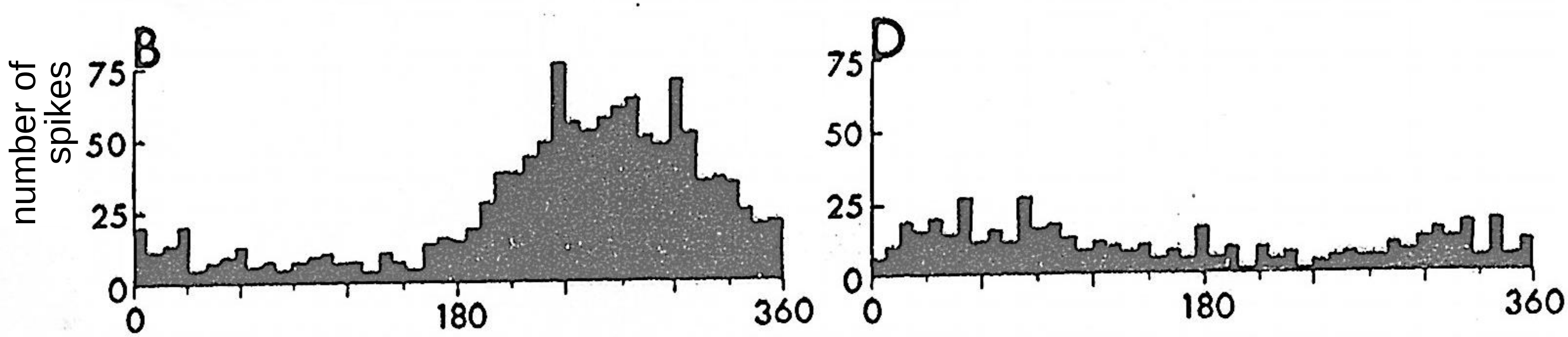
Registered signal in computer

Note that in this example the response always occurs at a phase of 180 degrees.

Phase locking in the barn owl

Phase locking can be measured by plotting spike arrival times with respect to the period of the stimulus tone.

5 kHz   Period 200 μs   9 kHz   Period 111 μs



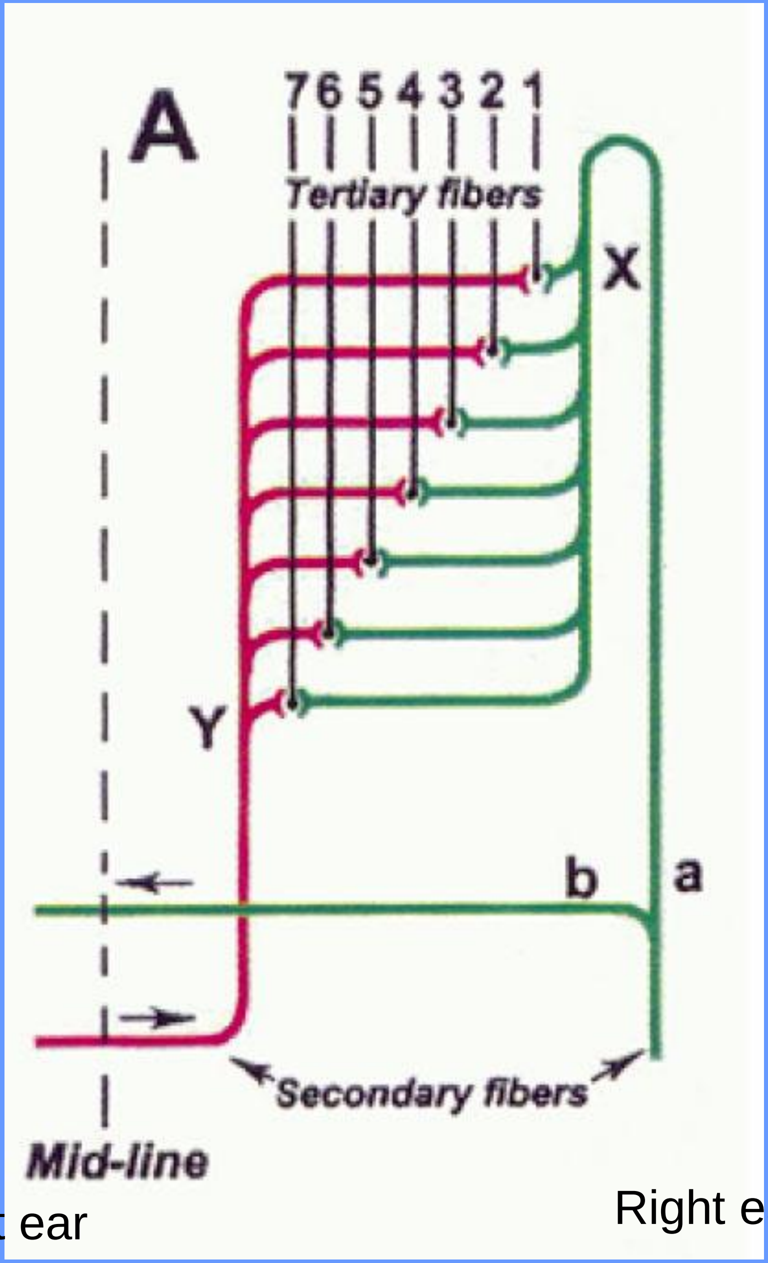
Stimulus phase in degrees

Precision of phase locking is 35 μs at 5 kHz (Koeppl (1997)).

Jefferess model (1948)

Coincident detector neurons

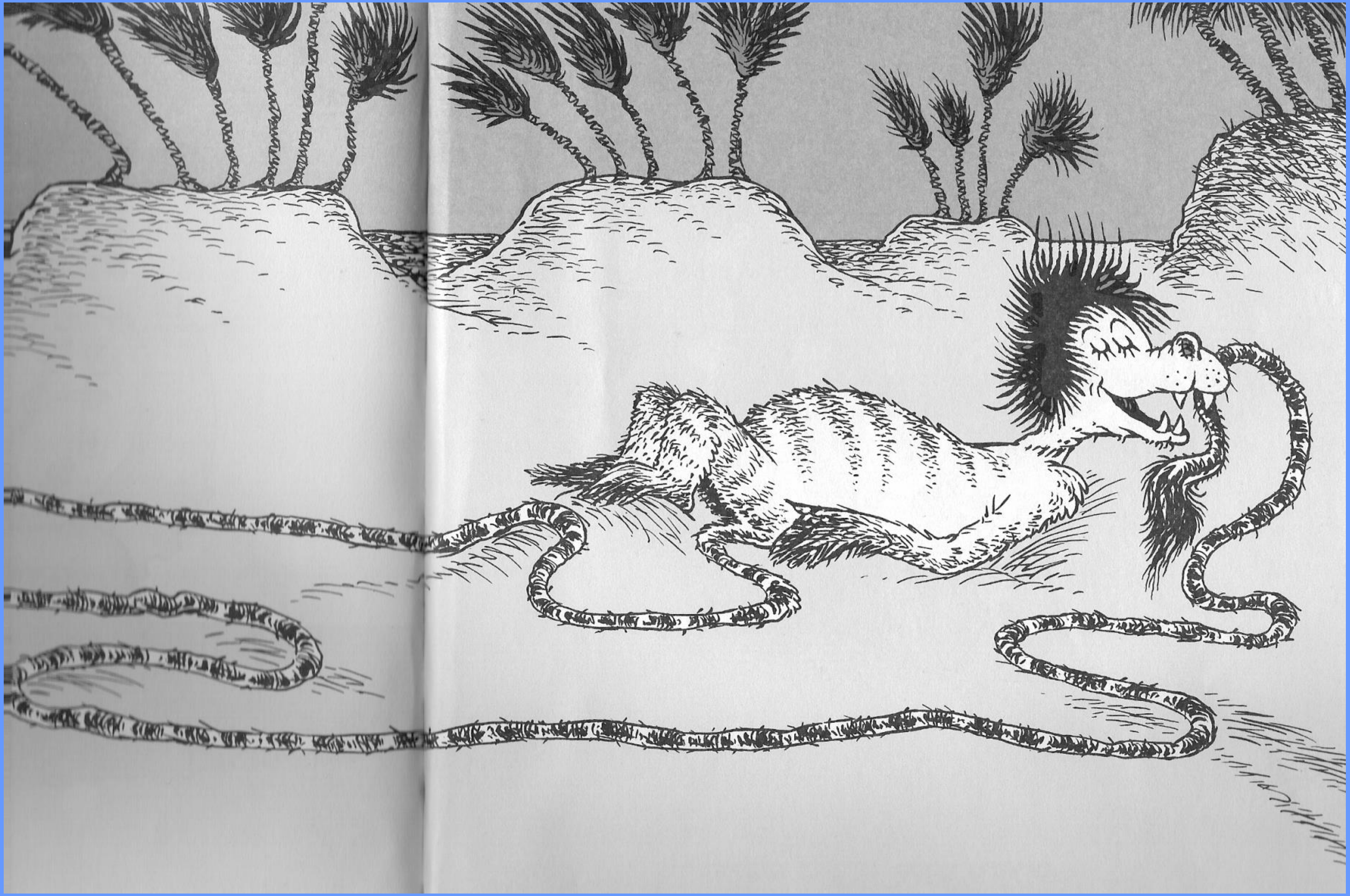
Jefferess model (1948)



left ear

Right ear

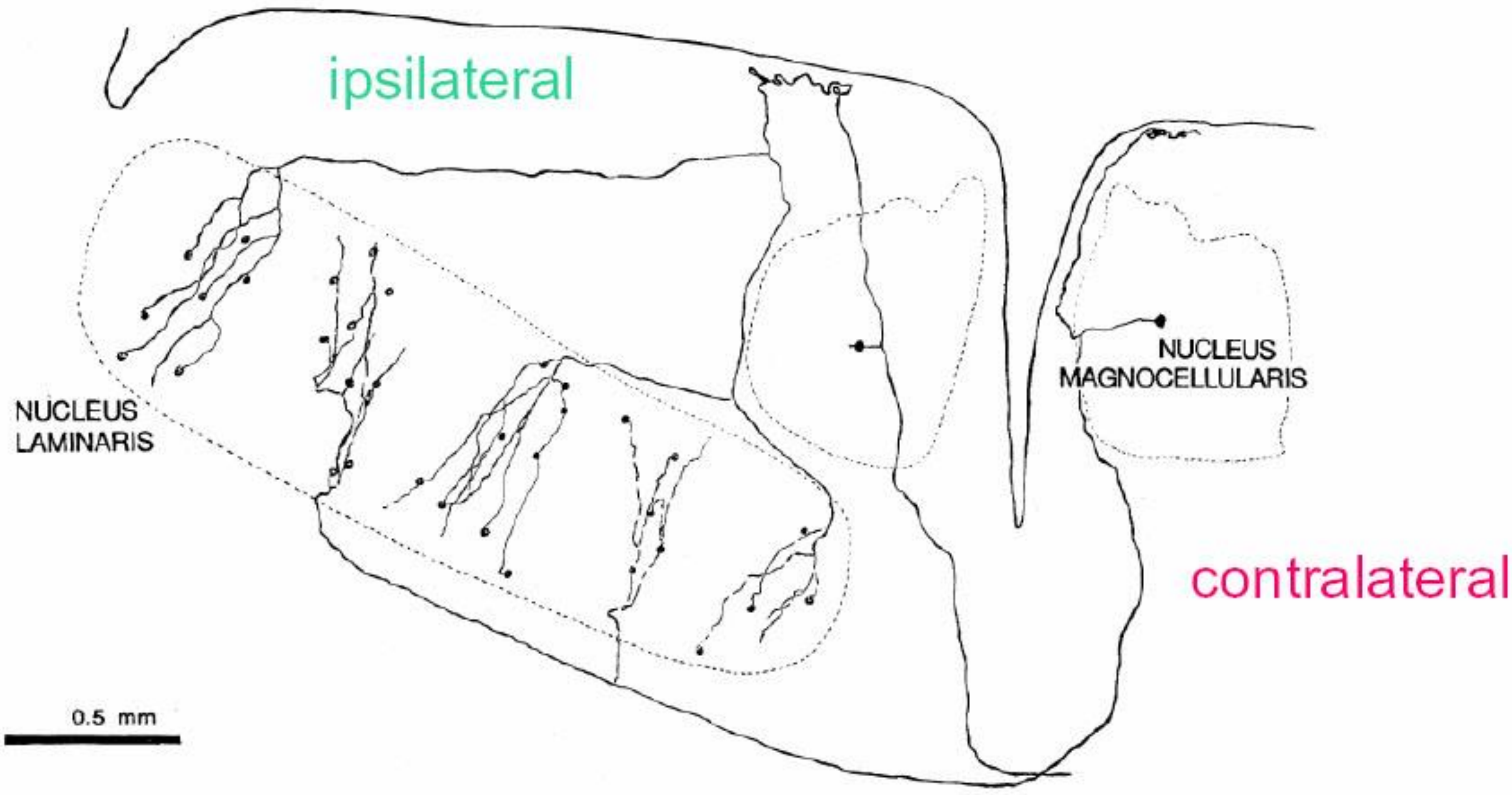
Delay lines



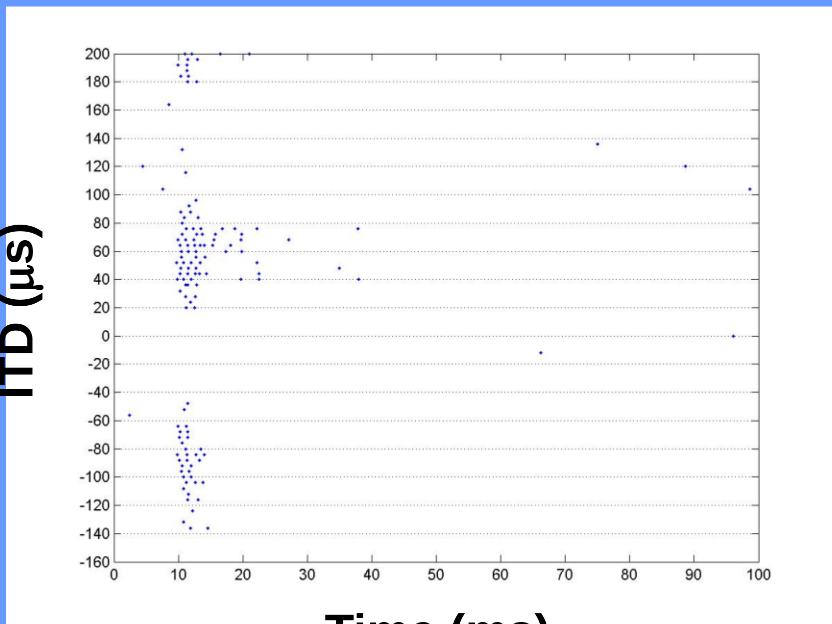
Does the brain computes ITDs as Jefferess suggested?

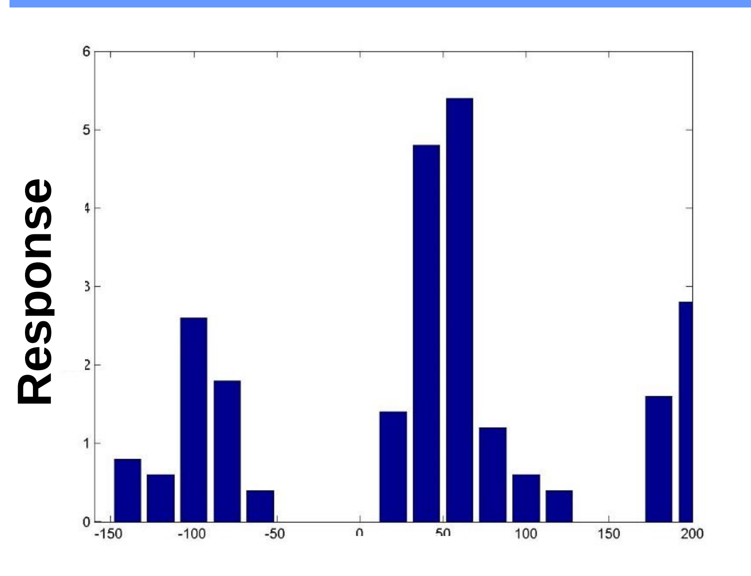
Nucleus Laminaris / Medial Superior Olive - sites of binaural convergence

Anatomical evidence for Jeffress model

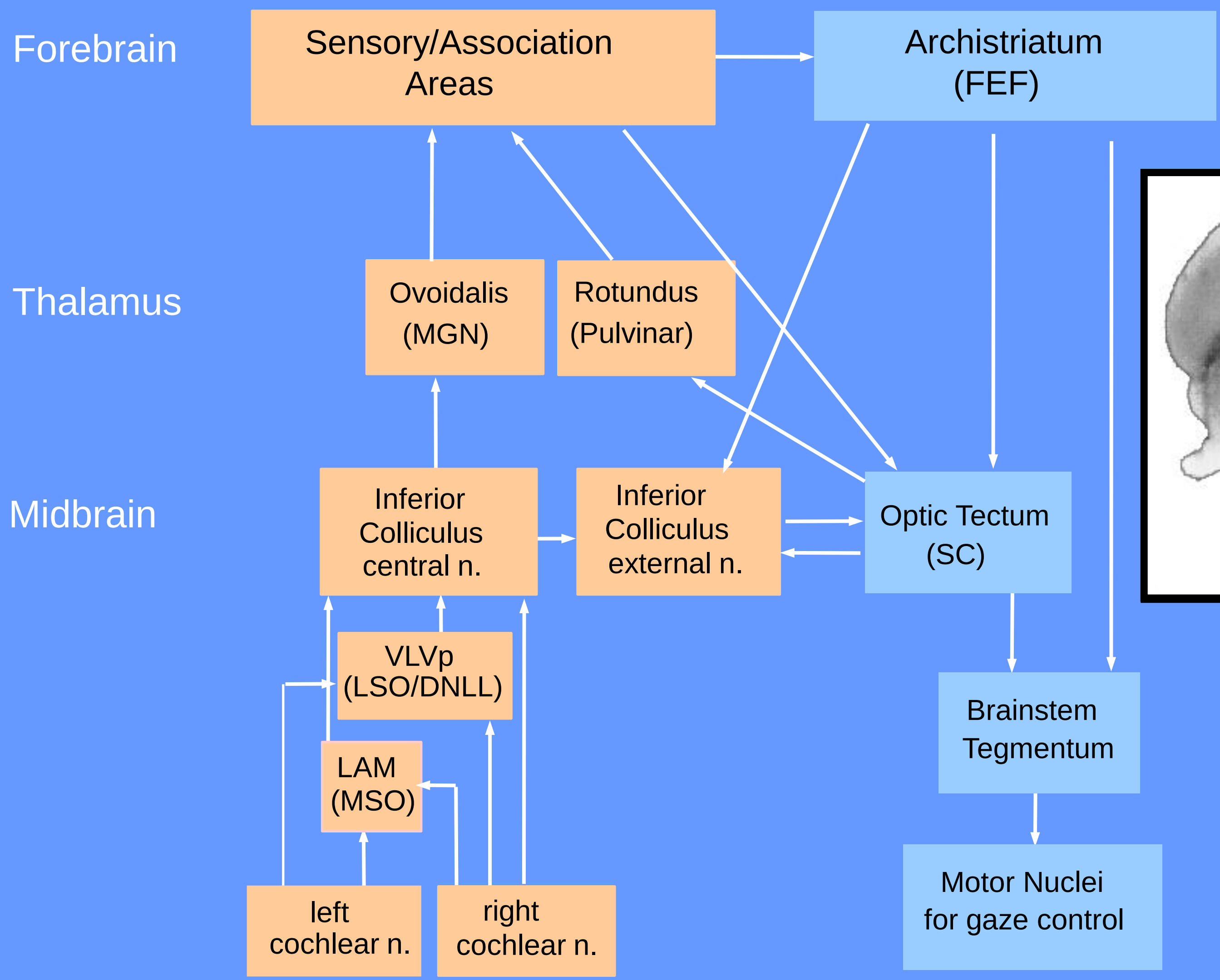


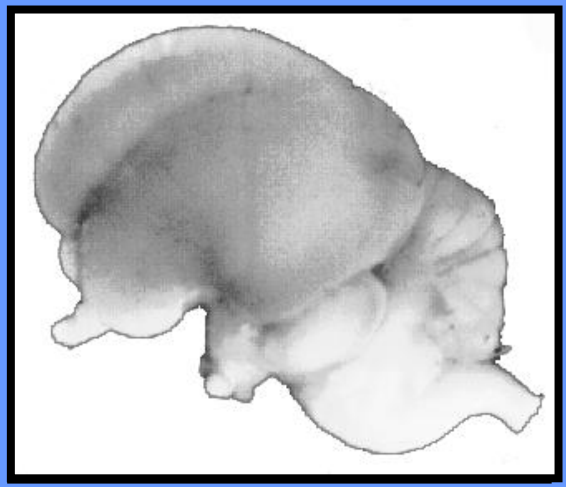
ITD curves in Inferior colliculus

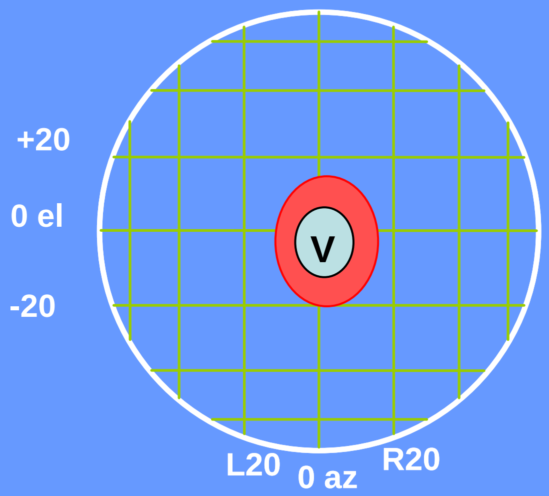


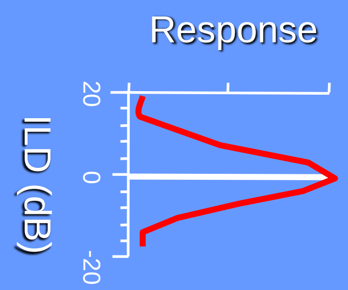


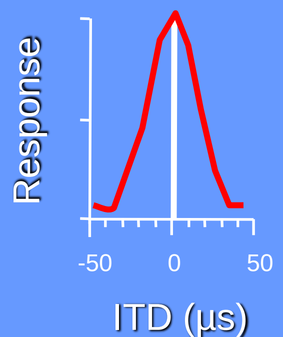
SOUND LOCALIZATION GAZE CONTROL

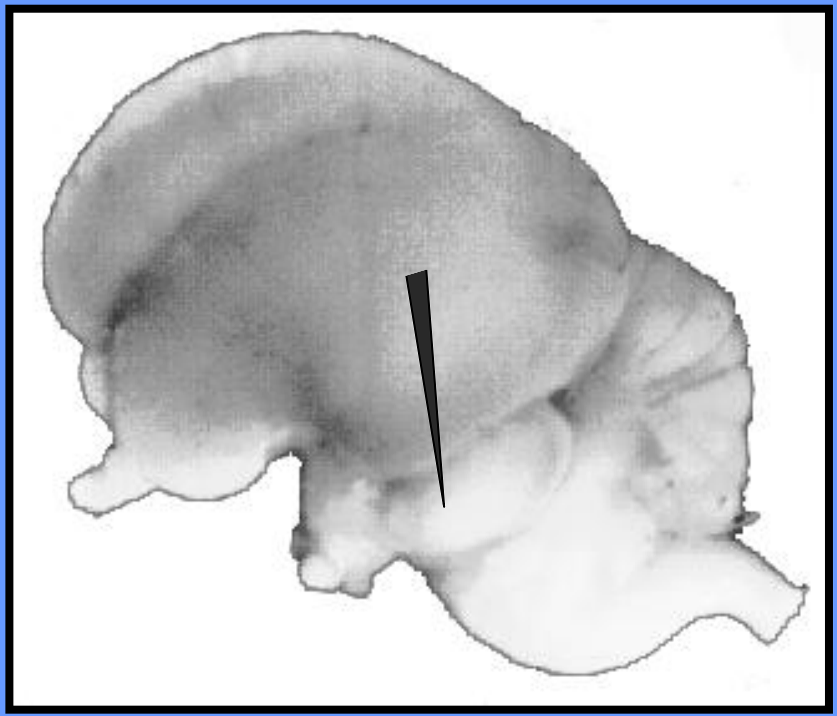


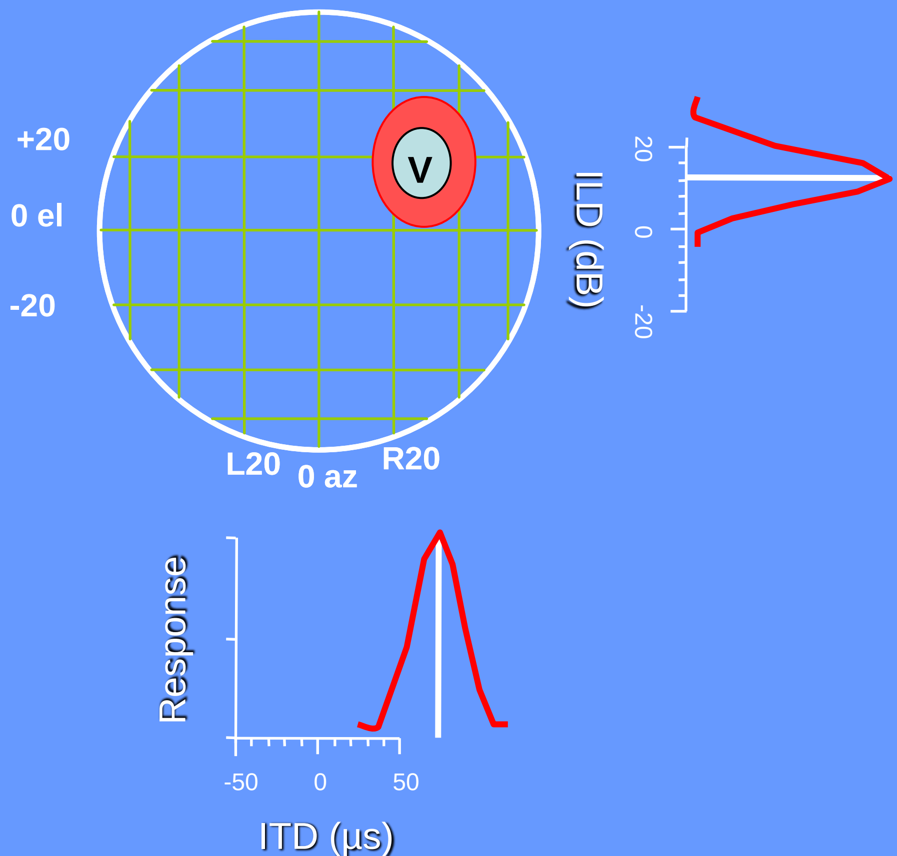


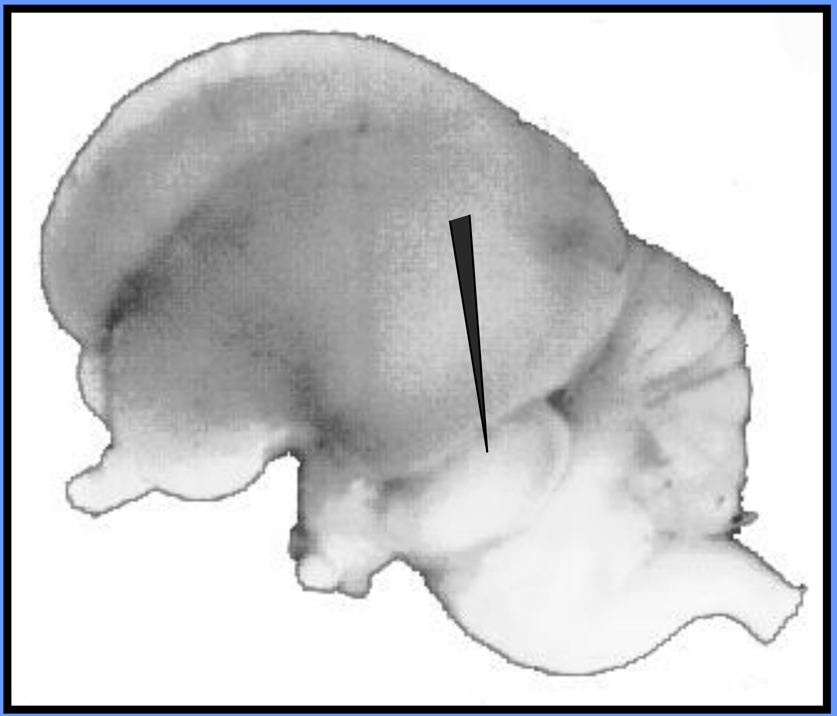

+20
0 el
-20
V
L20
0 az
R20


Response
ILD (dB)
20
0
-20

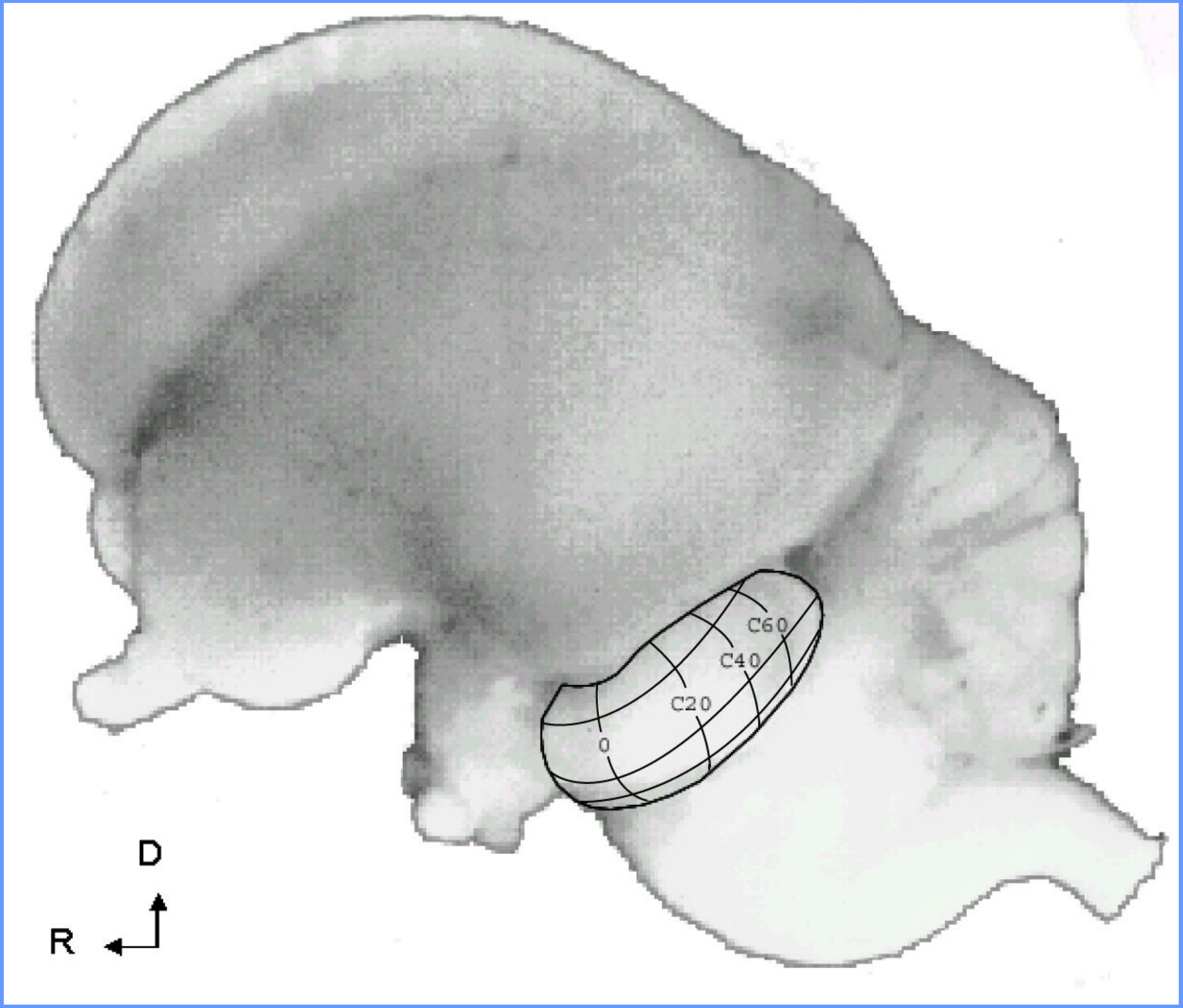

Response
-50
0
50
ITD (µs)



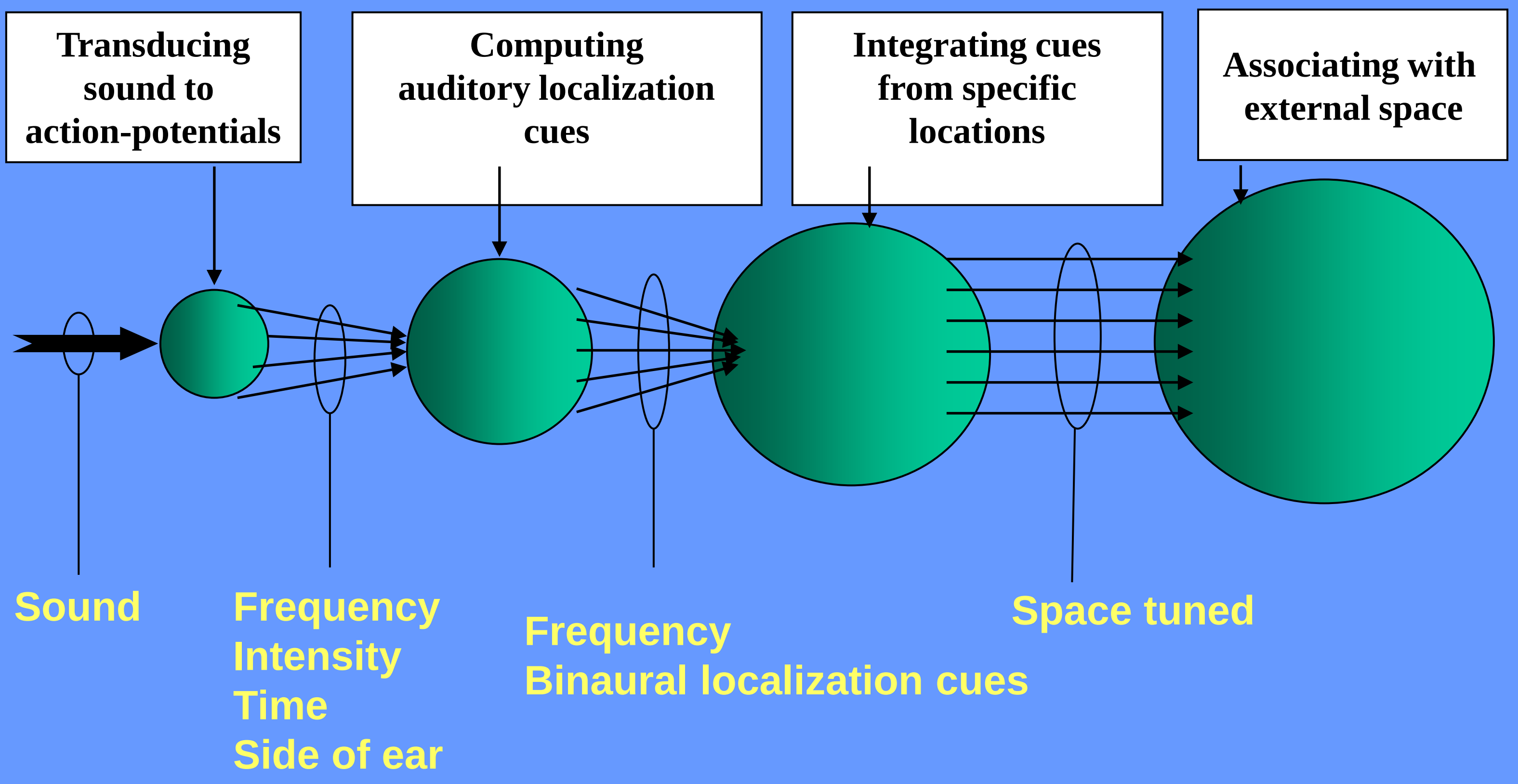

+20
0 el
-20
V
L20
0 az
R20
ILD (dB)
20
0
-20
Response
-50
0
50
ITD (μs)



Visual and auditory maps in the OT

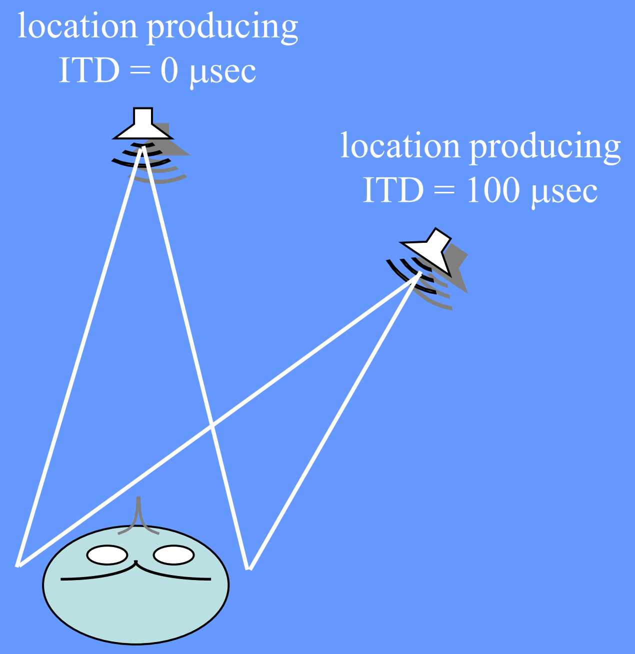


Computational map

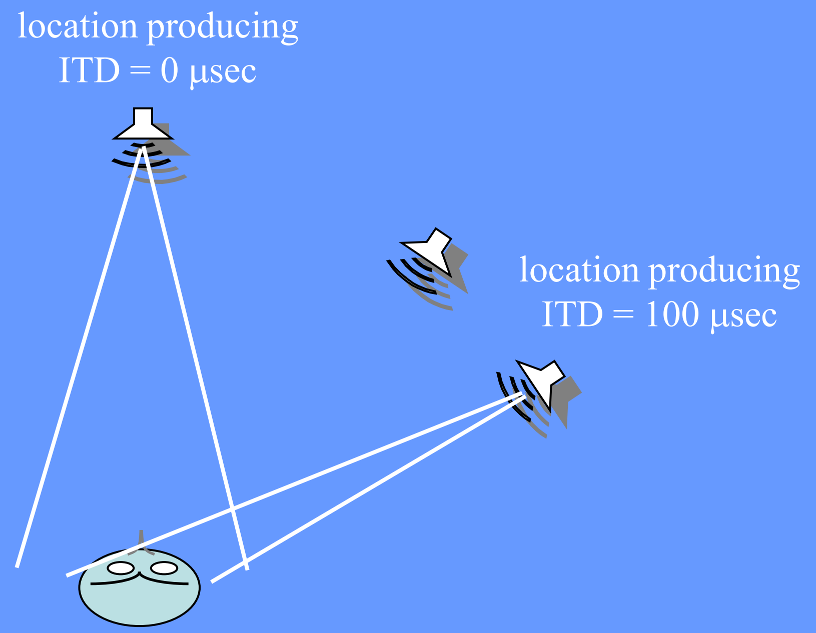


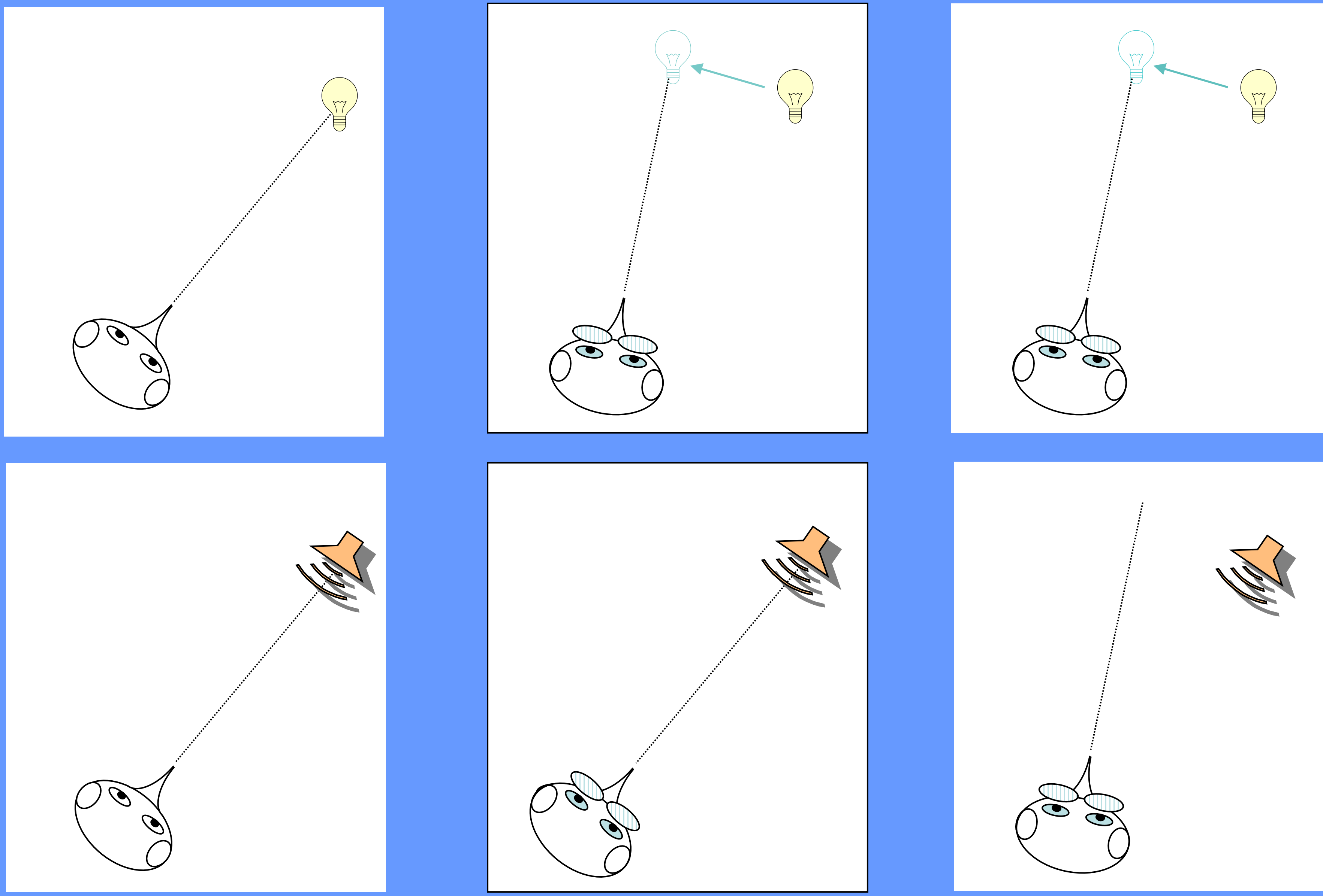
Computational maps

The matching problem



Computational maps
The matching problem



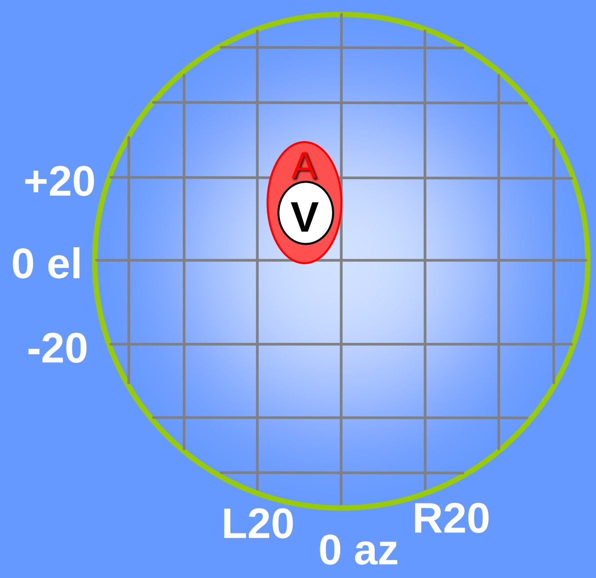


Normal | **Immediate Effect of Prisms** | **Prism-adapted**

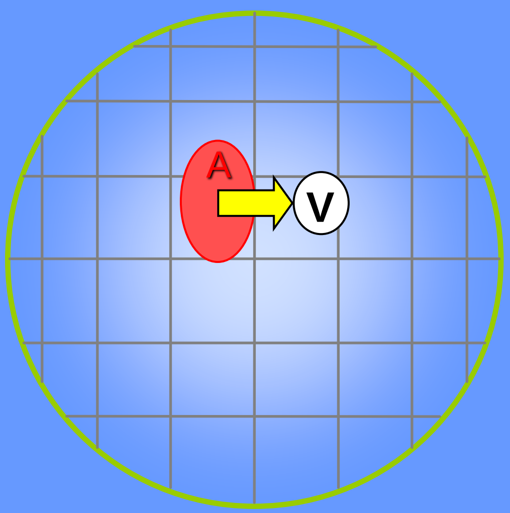
Knudsen and Knudsen J Neurosci (1989)

Effect of prism experience on auditory tuning

Normal

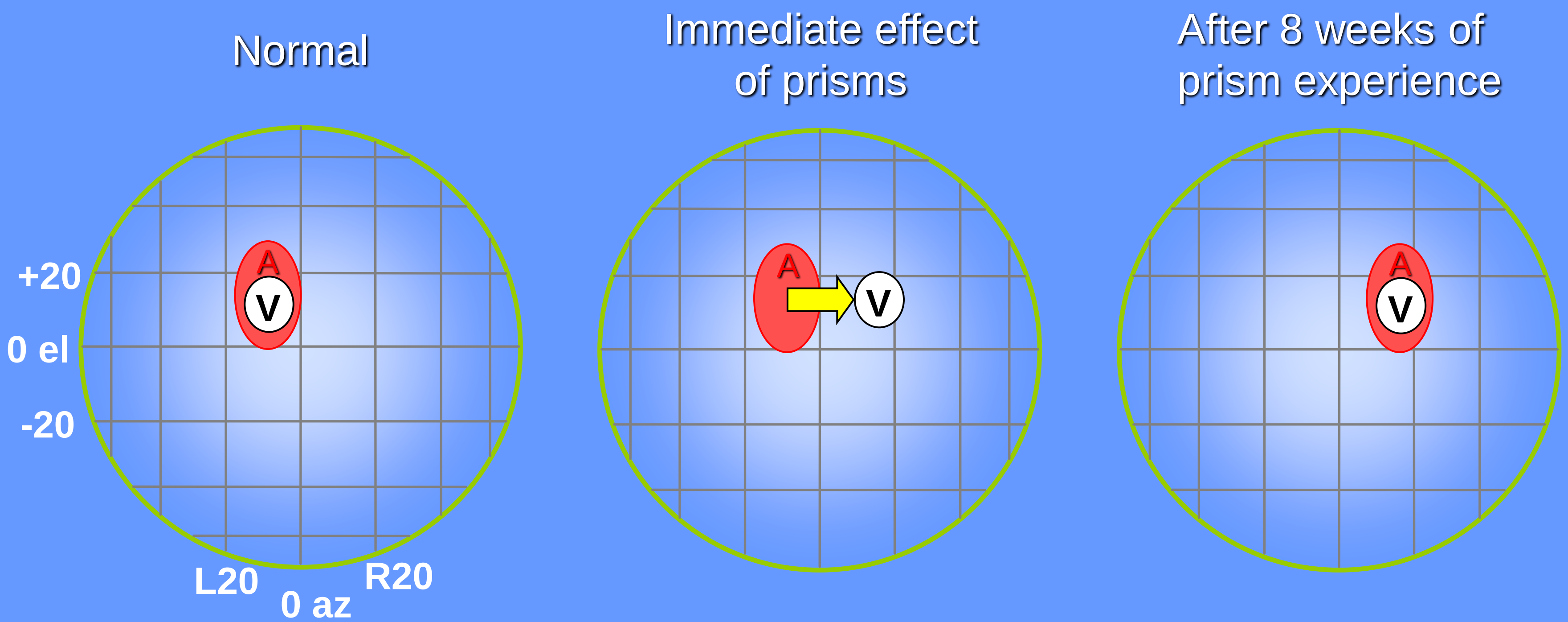


Immediate effect
of prisms



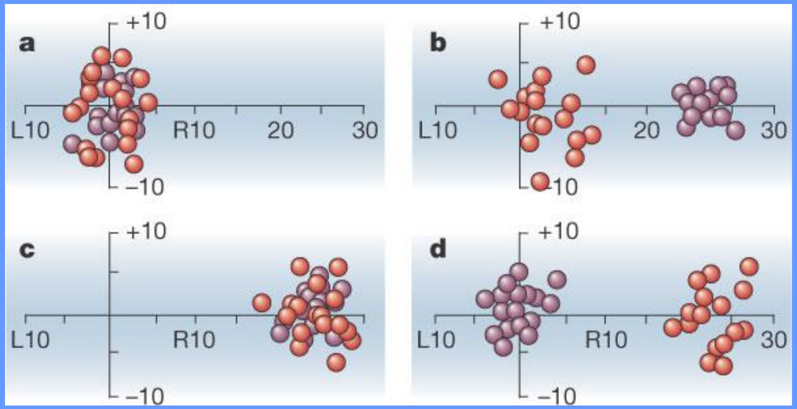
Knudsen and Brainard, Science (1991)

Effect of prism experience on auditory tuning

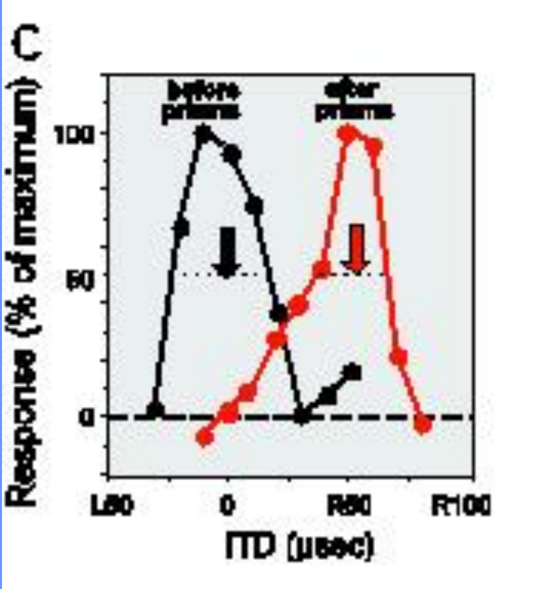


Quantification of learning

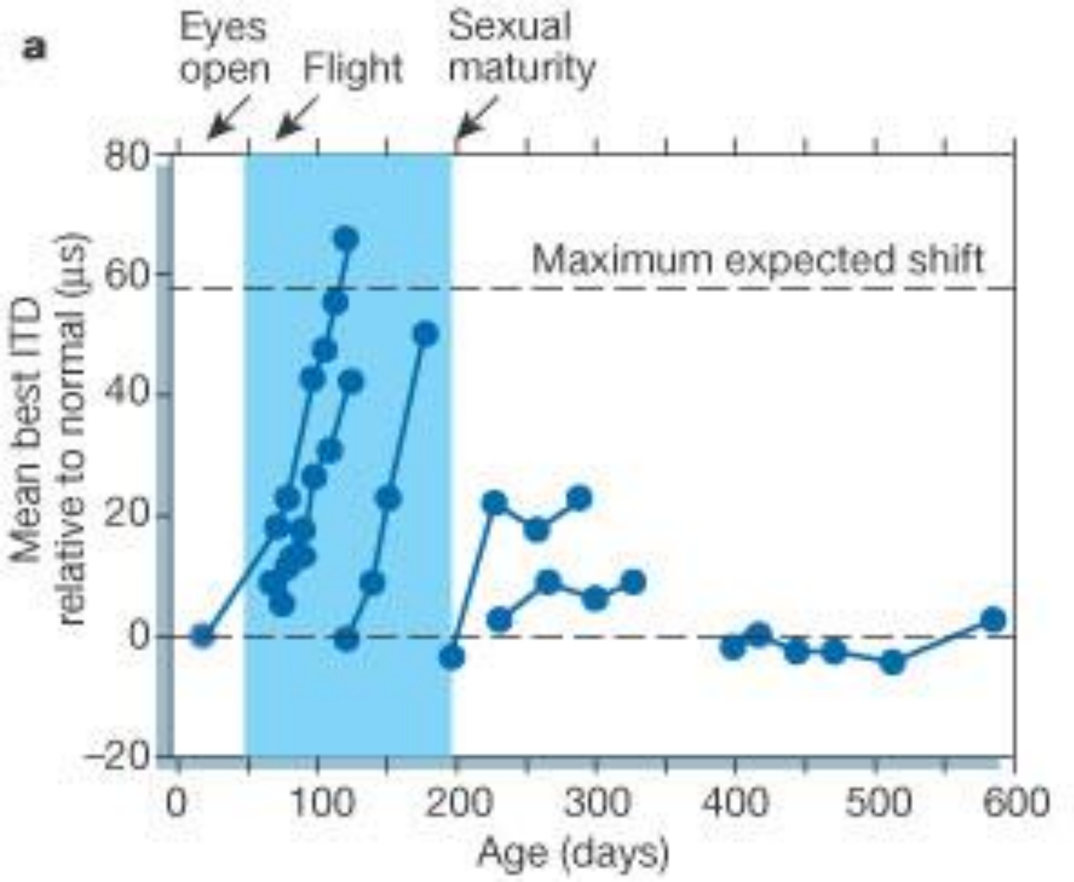
1. Behavioral test



2. Physiological test



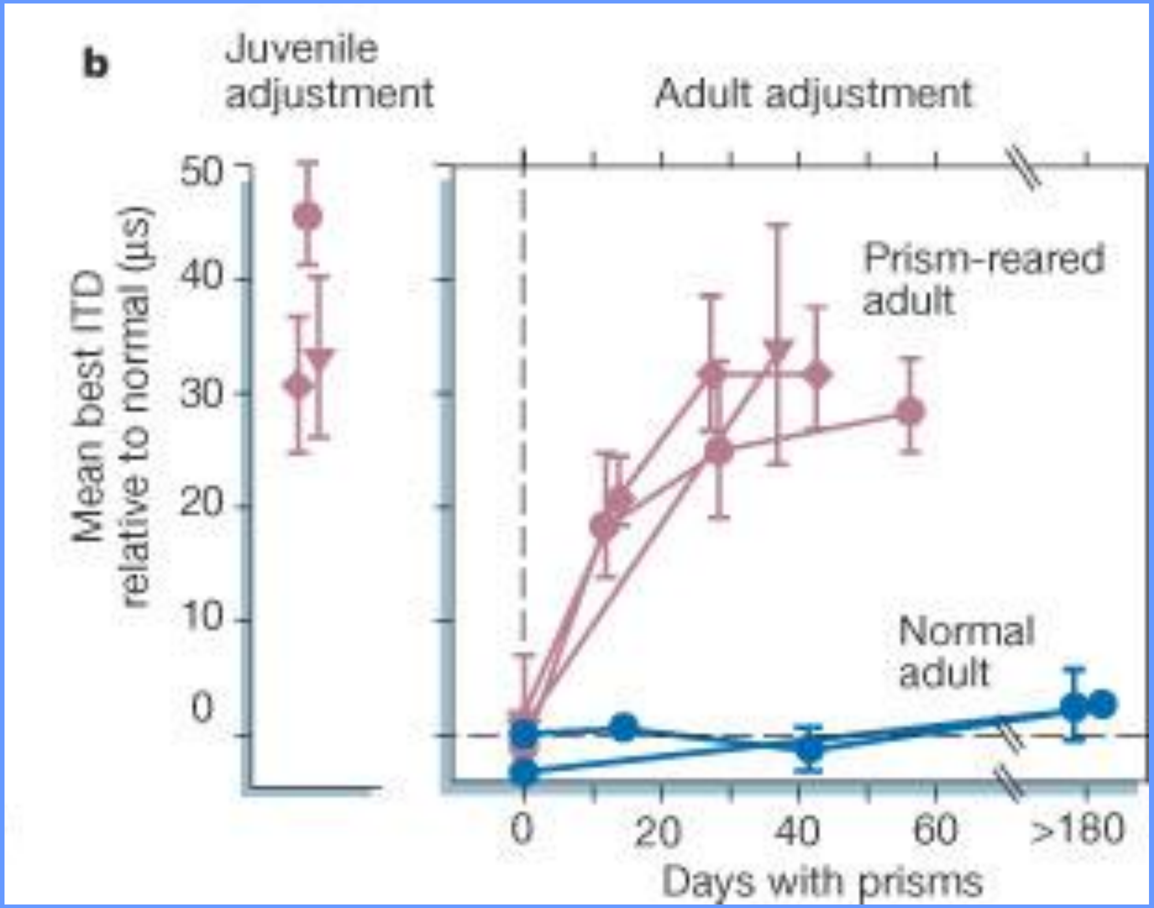
Decline in learning with age



67.

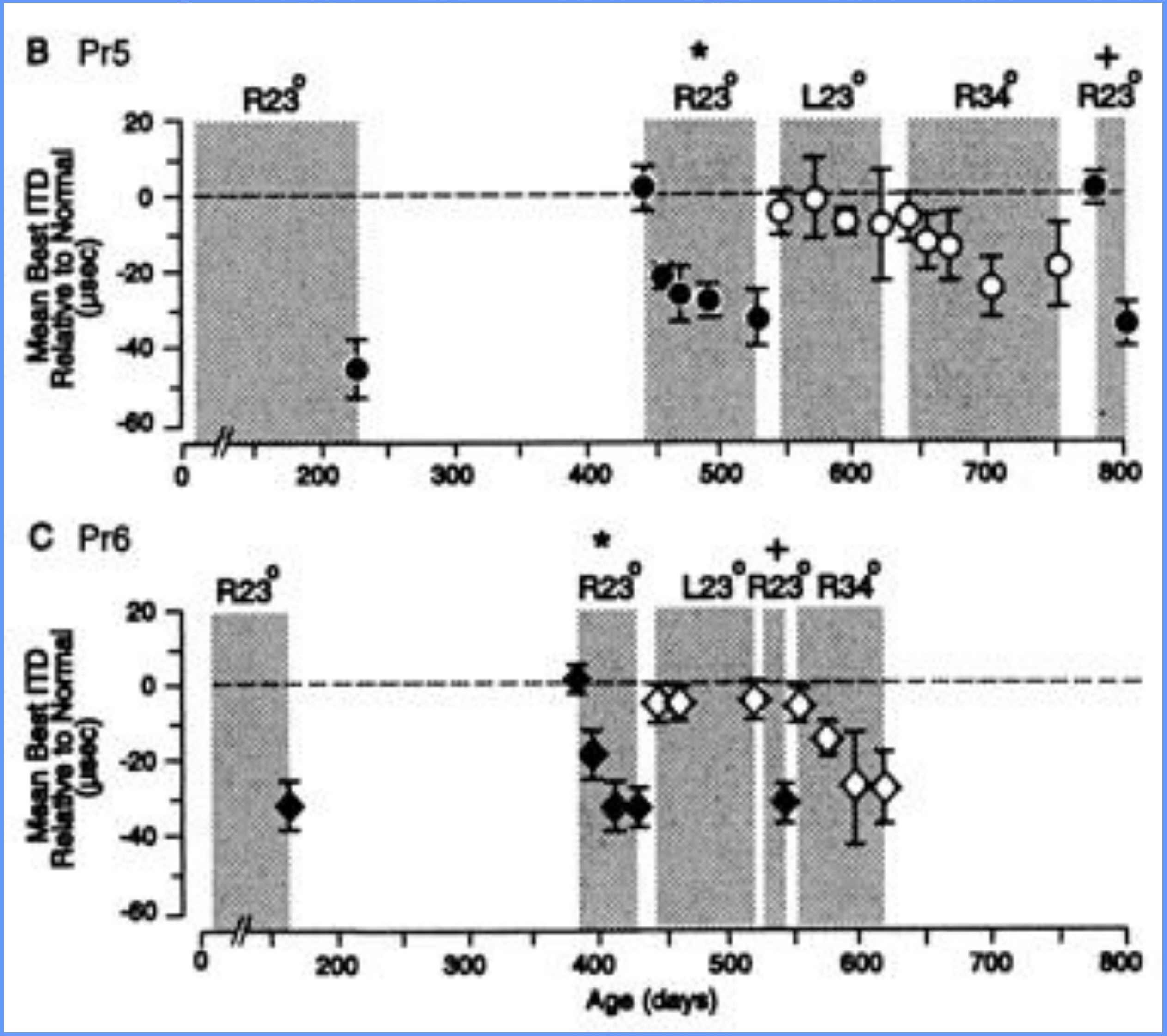
Knudsen, E. I. *Science*.(1998)

Increased capacity for learning in adults that have had appropriate experience as juveniles



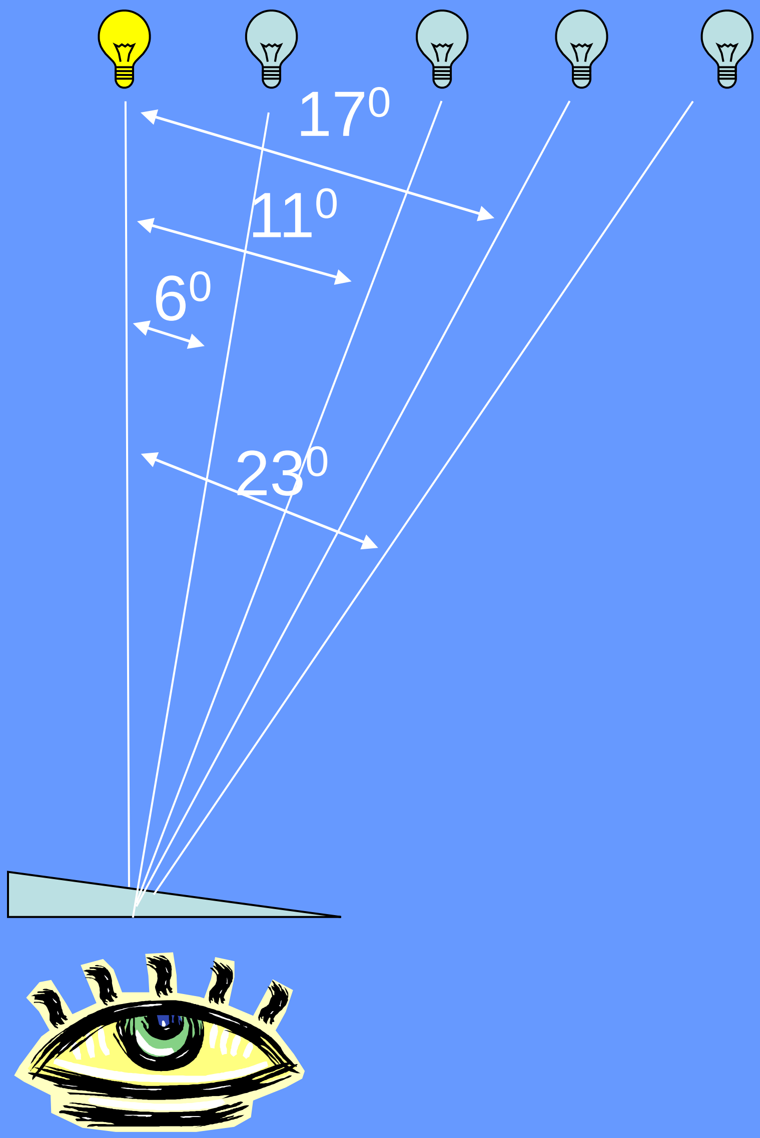
67. Knudsen, E. I. *Science*.(1998)

Effects of juvenile experience on adult learning

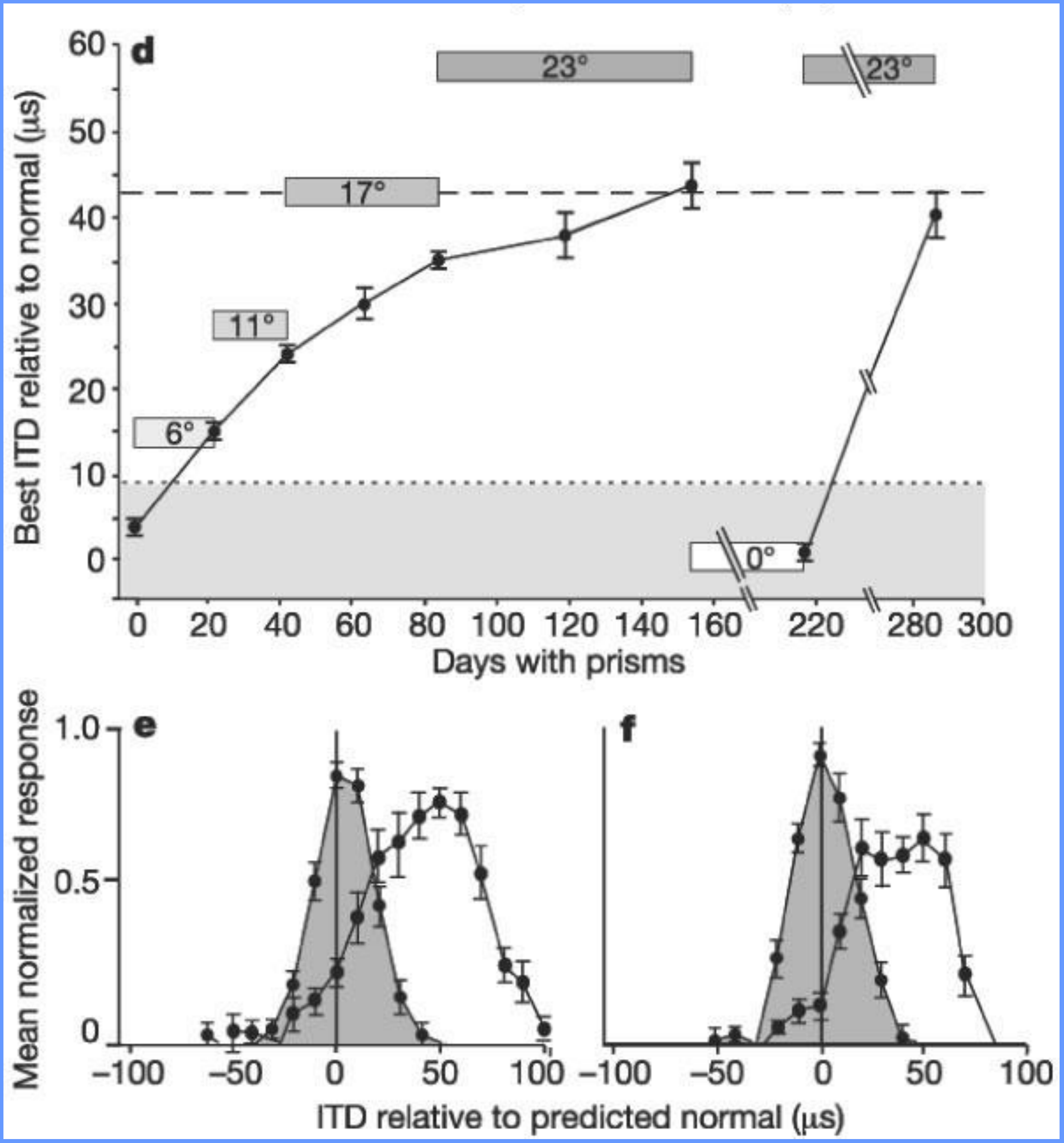


 Knudsen, E. I. *Science*.(1998)

Incremental learning

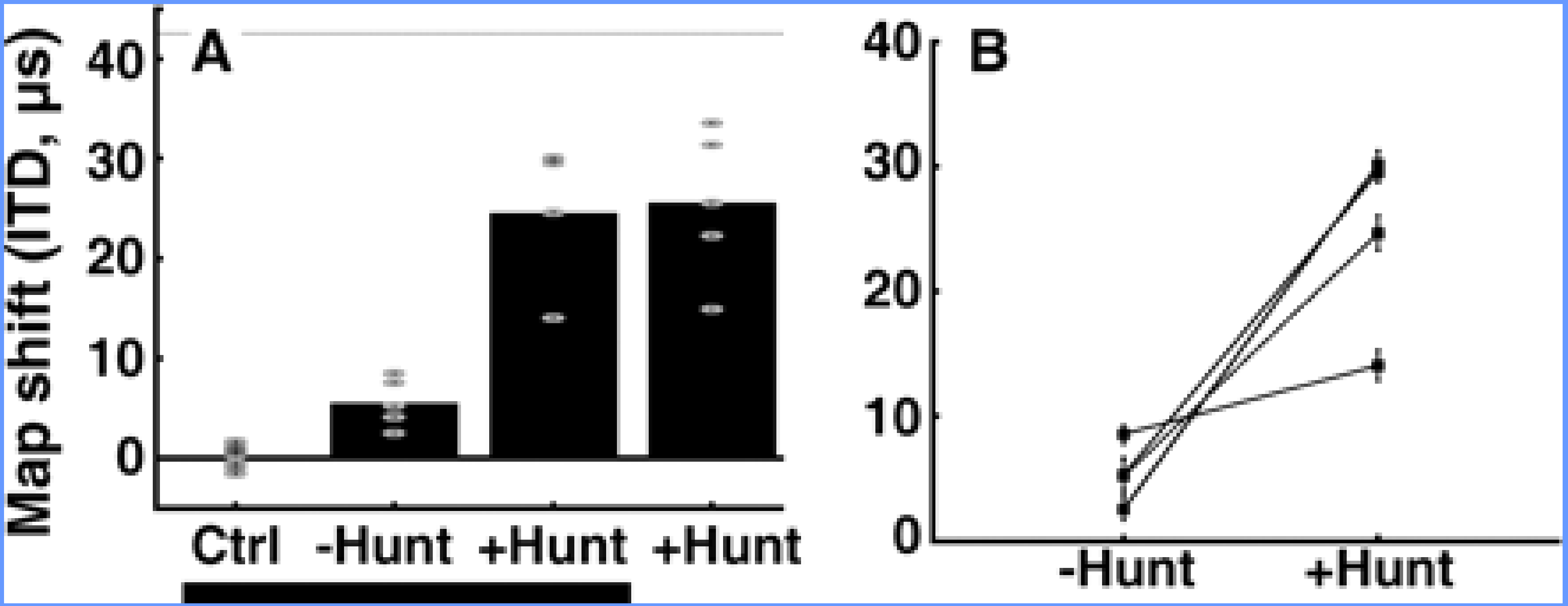


Incremental learning



Linkenhoker and Knudsen (2002) Nature

Rich and lively experiences increase learning capacity in adults

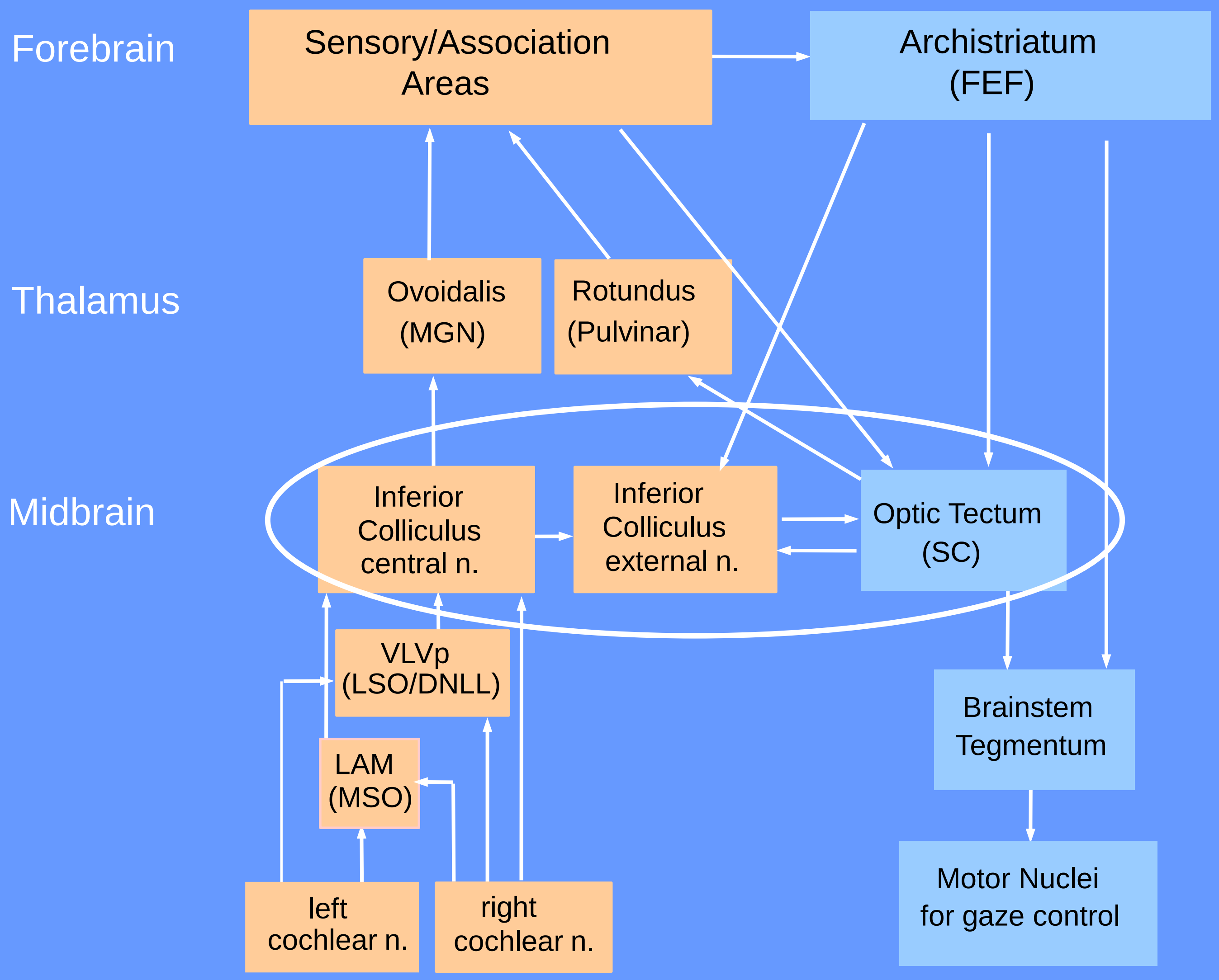


Bergan et al., Journal of Neuroscience (2005)

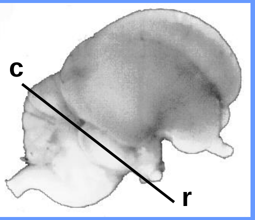
Summary

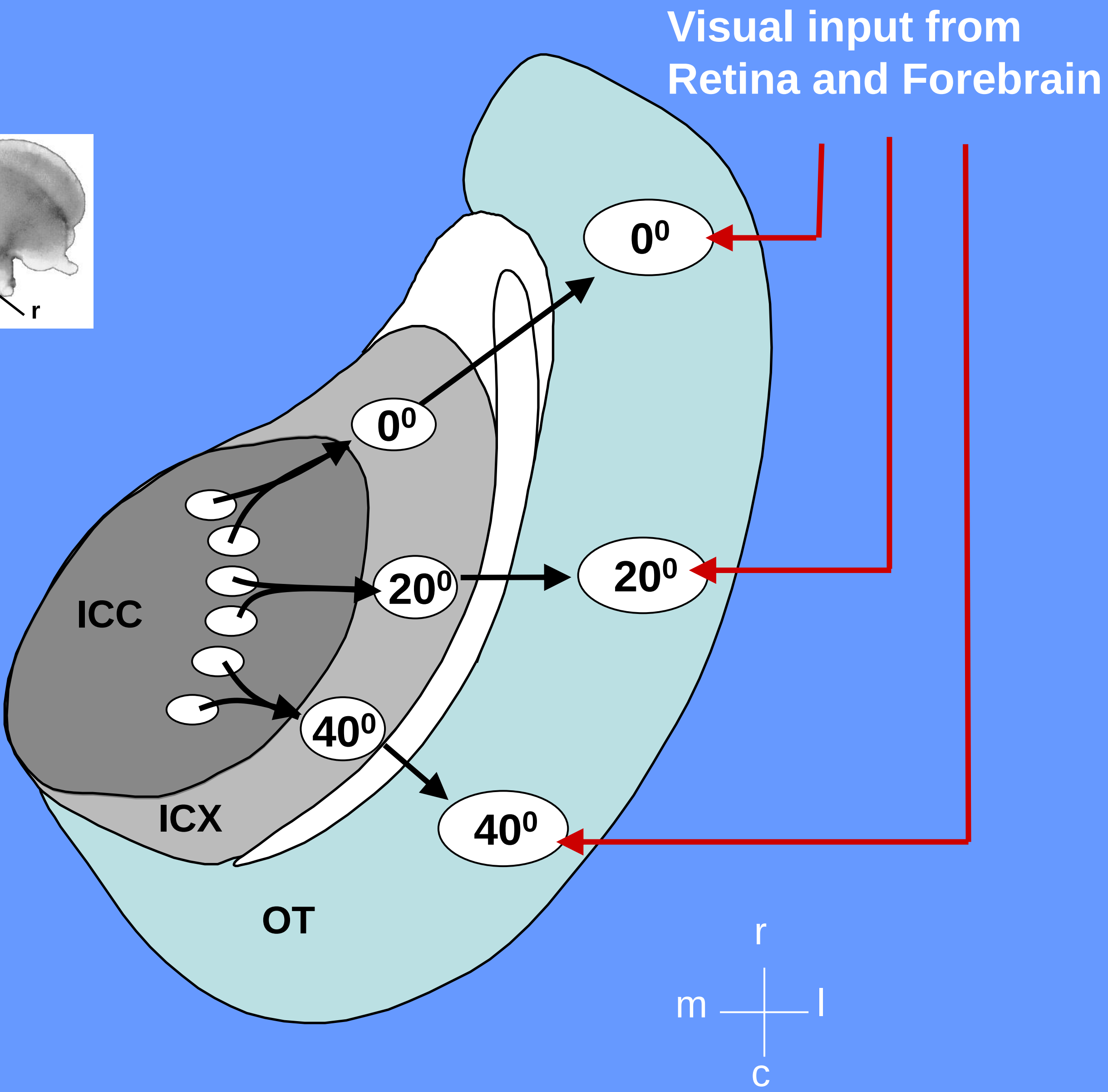
- Decline in learning with age
- Increased capacity for learning in adults that have had appropriate experience as juveniles
- Incremental training improves learning
- Rich and lively experiences increase learning capacity in adults

Where is the site of plasticity?

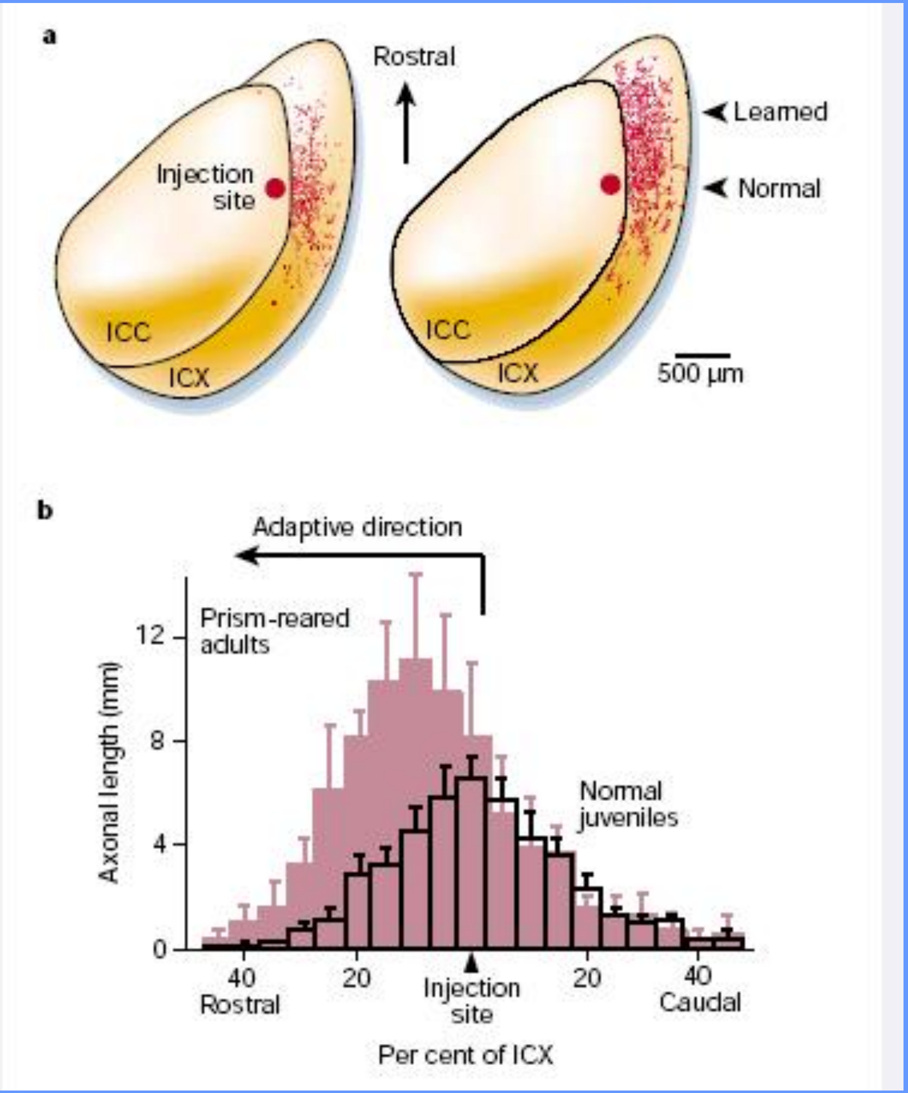


Horizontal section through the tectal lobe



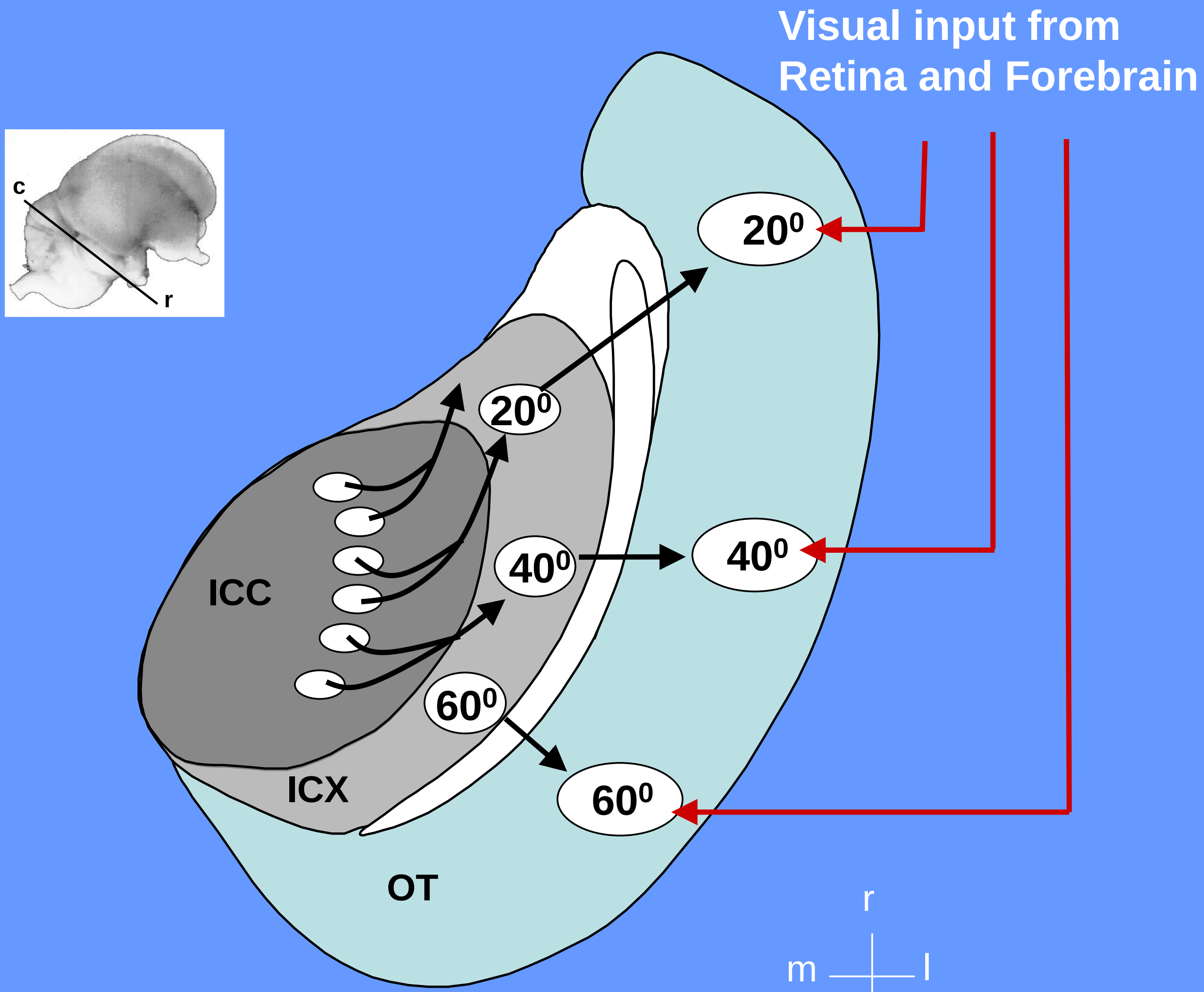


Site of plasticity in the ICX



Debello et al., J. Neurosci. 2001

After prism learning



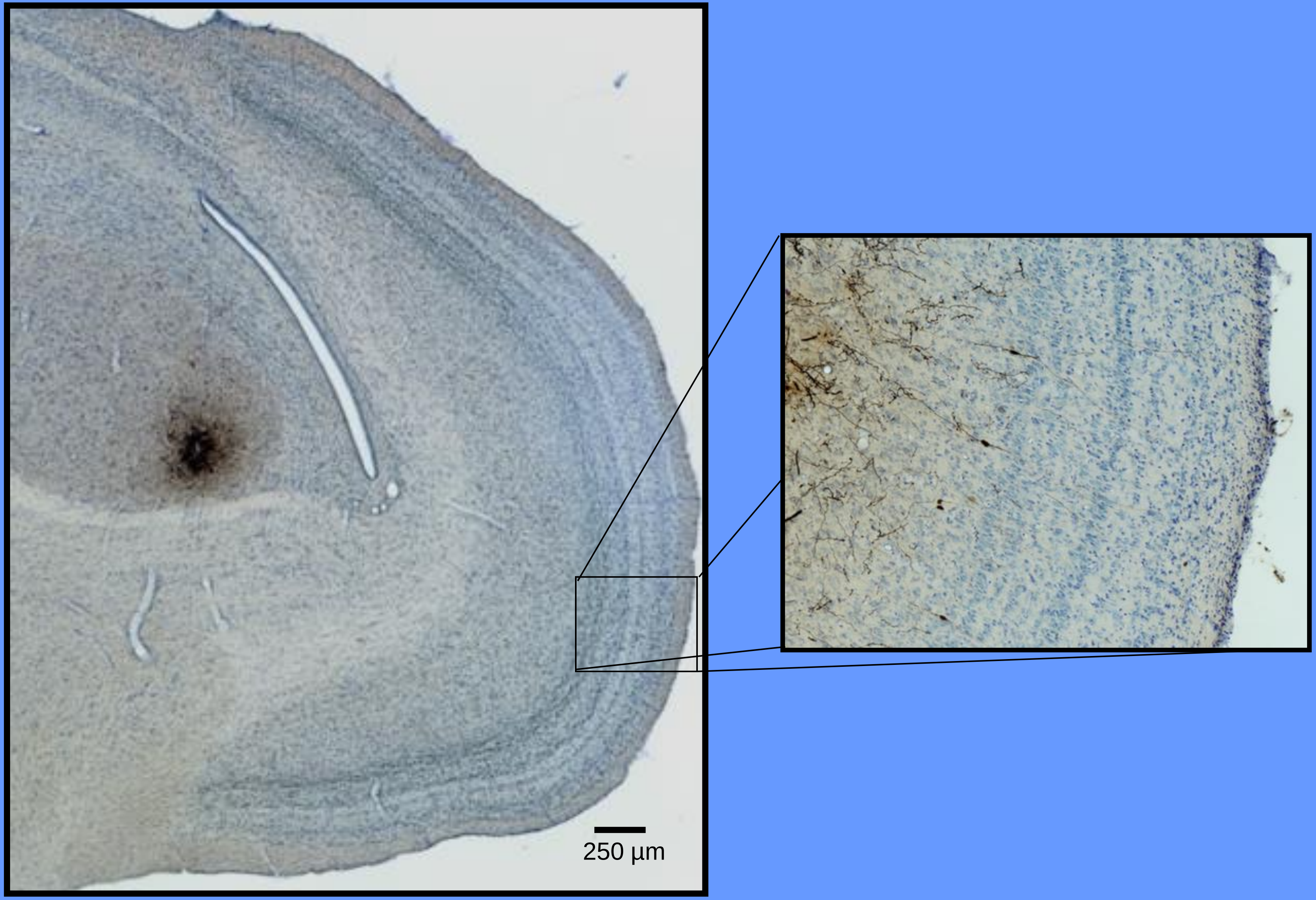
The instructive signal

- Operates in the ICX

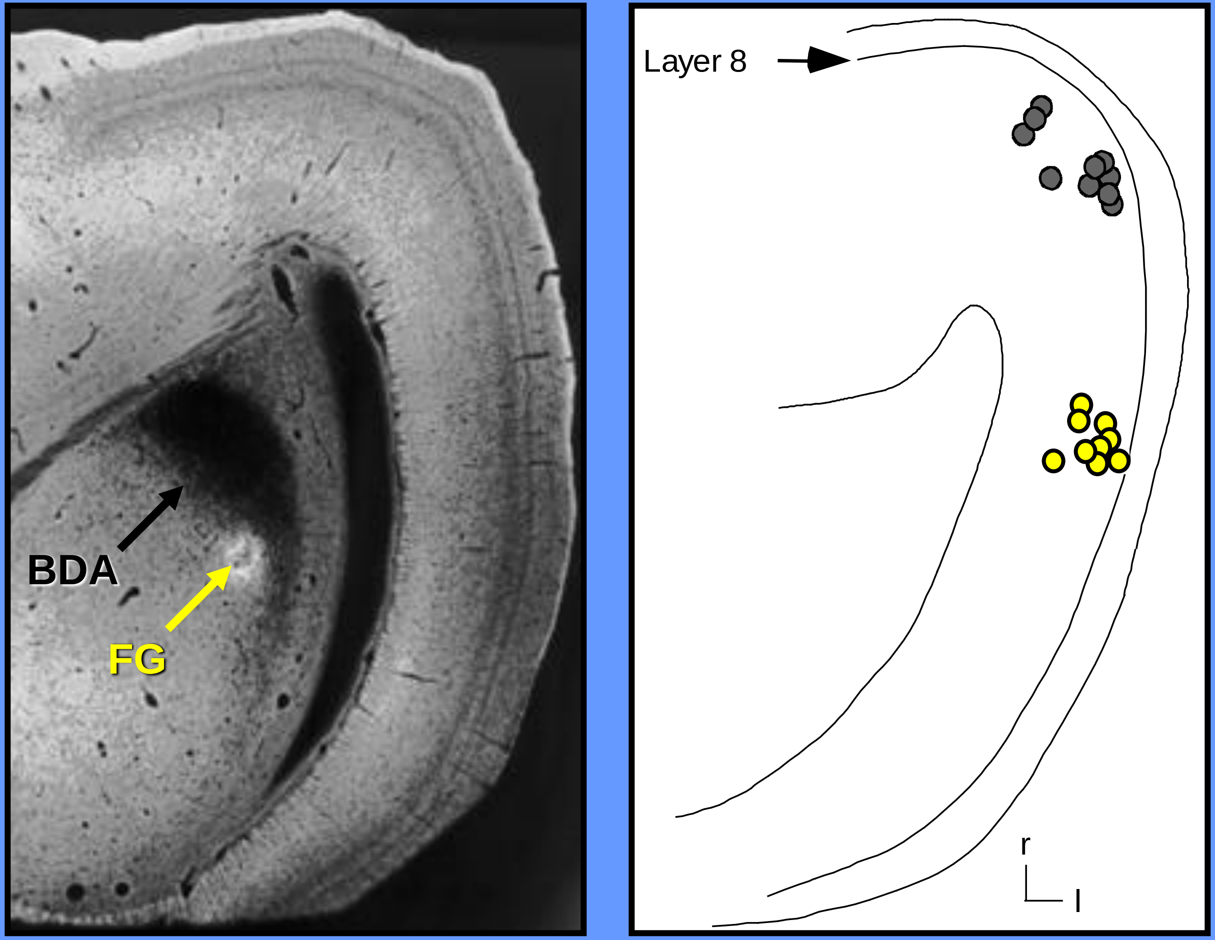
- Visually based

Where is the instructive signal coming from?

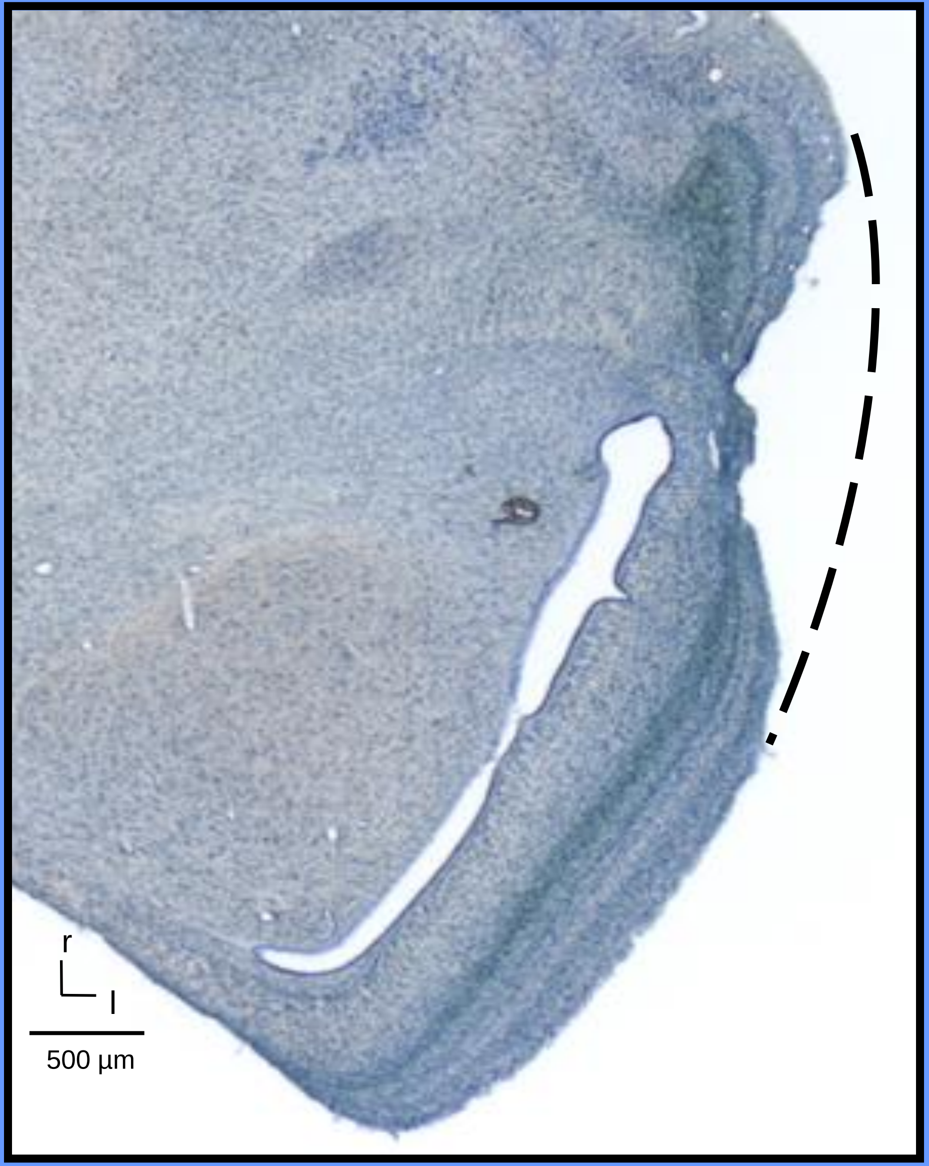
BDA injection site in ICX



Topography of the OT-ICX projection

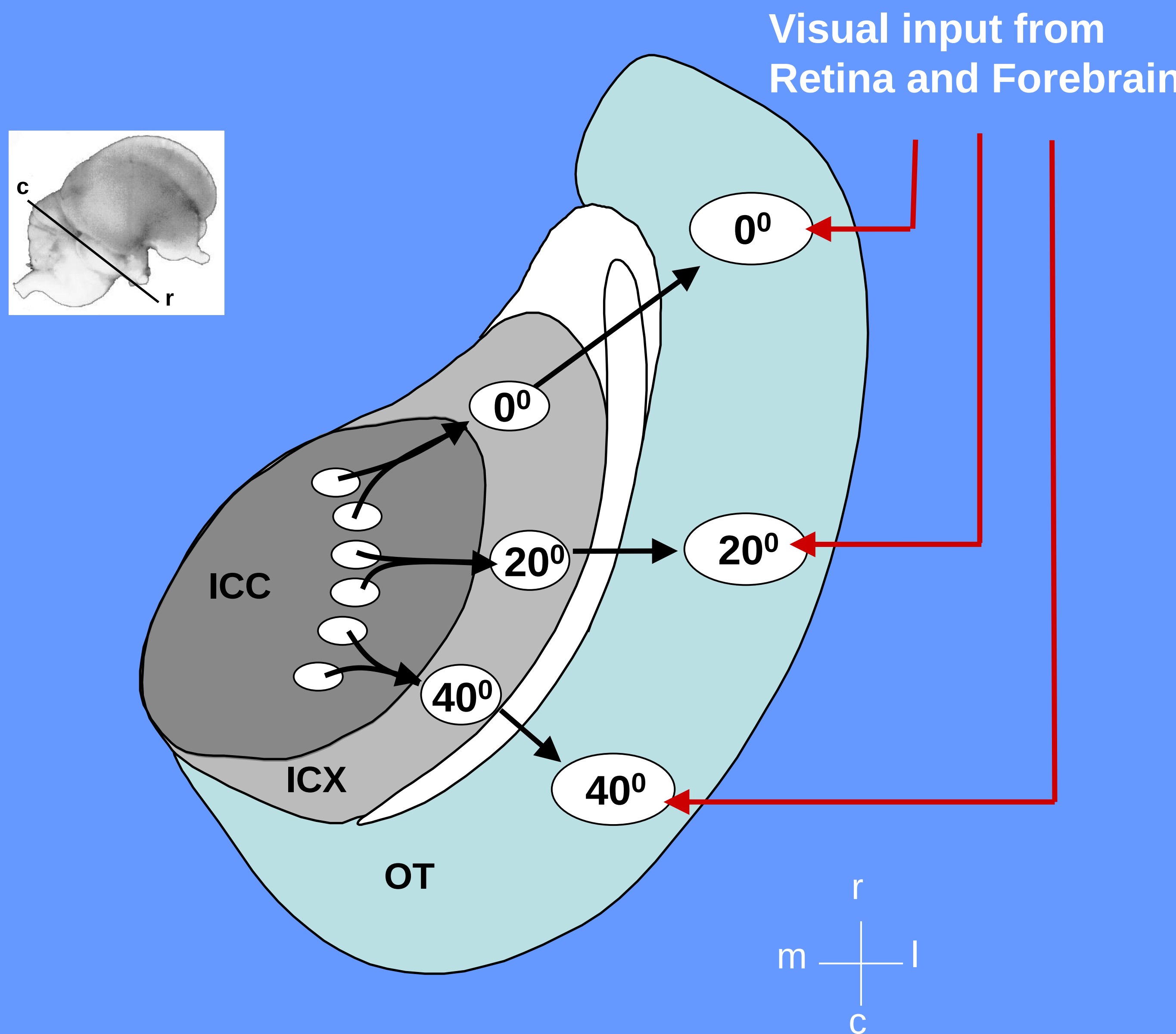


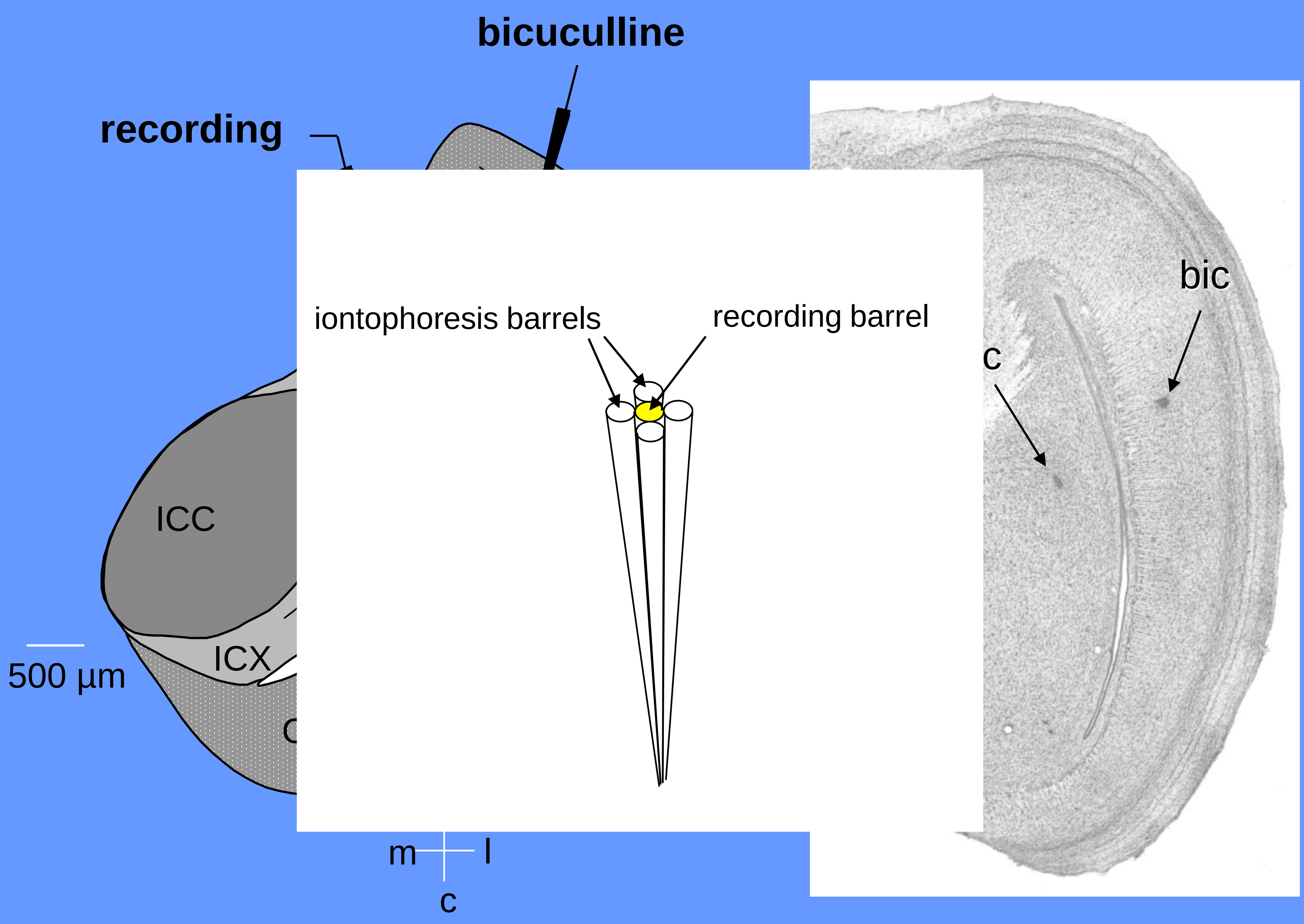
Restricted lesion of the optic tectum



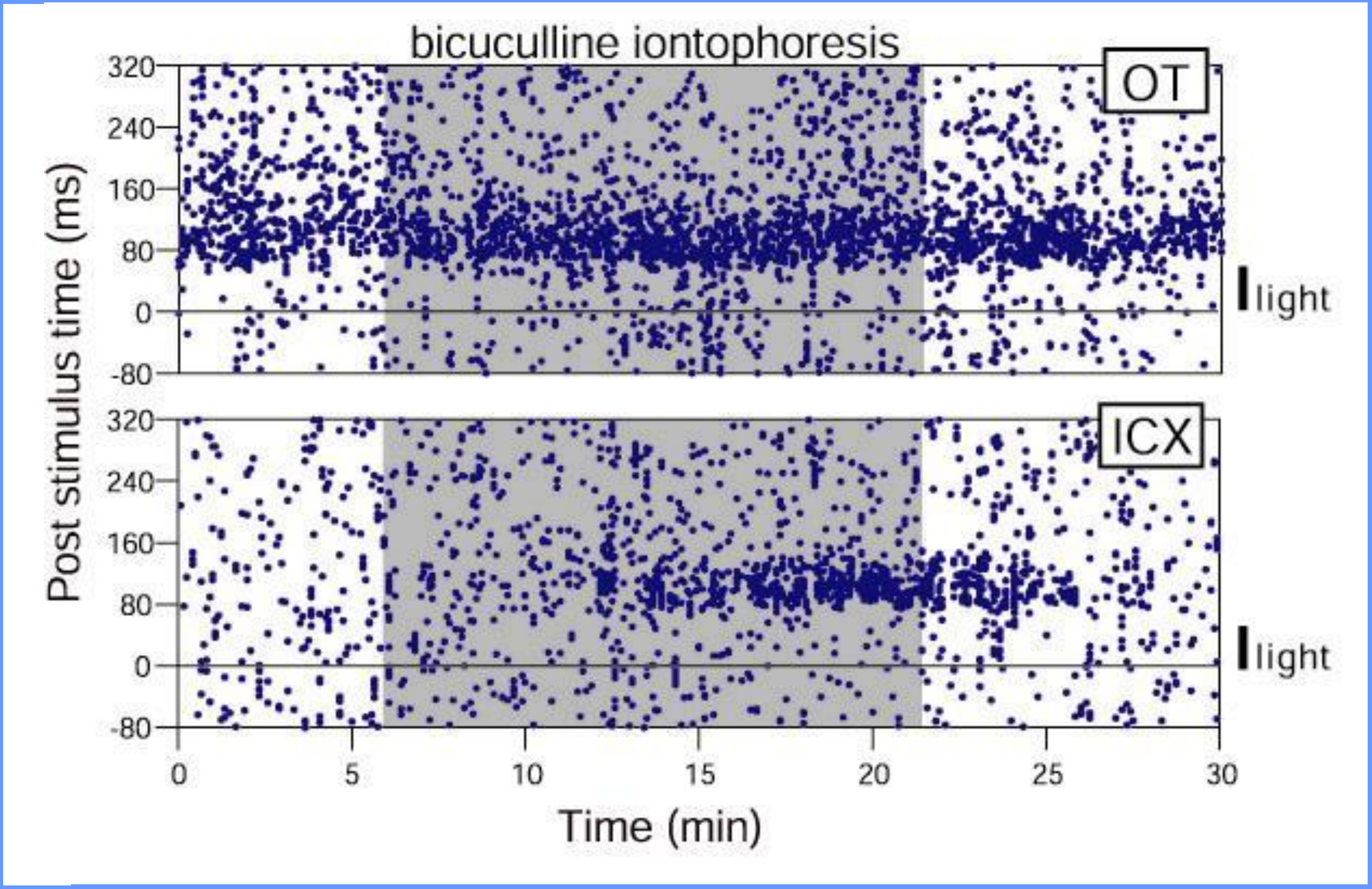
How can a visually based instructive signal act in an auditory structure?

Horizontal section through the tectal lobe

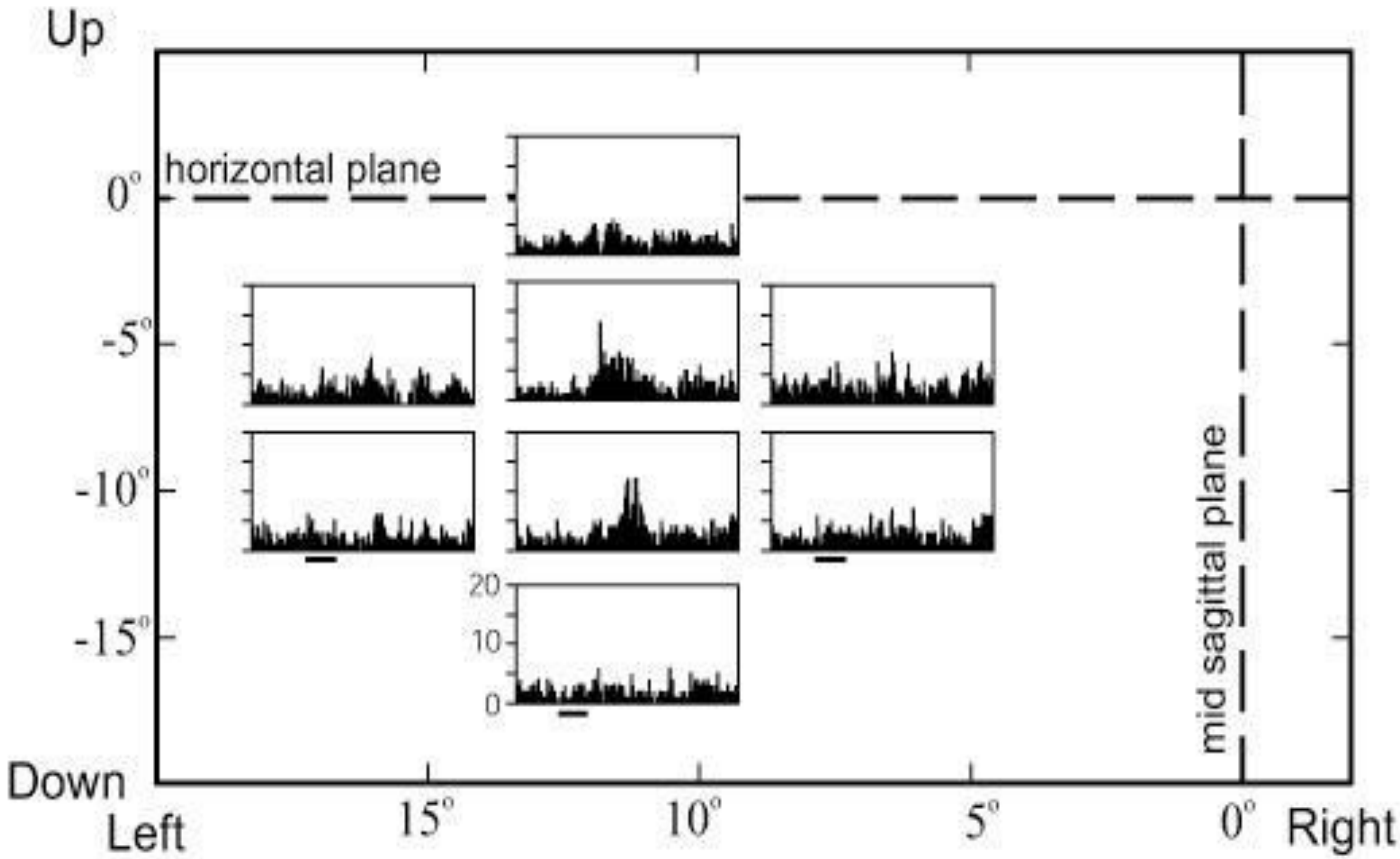


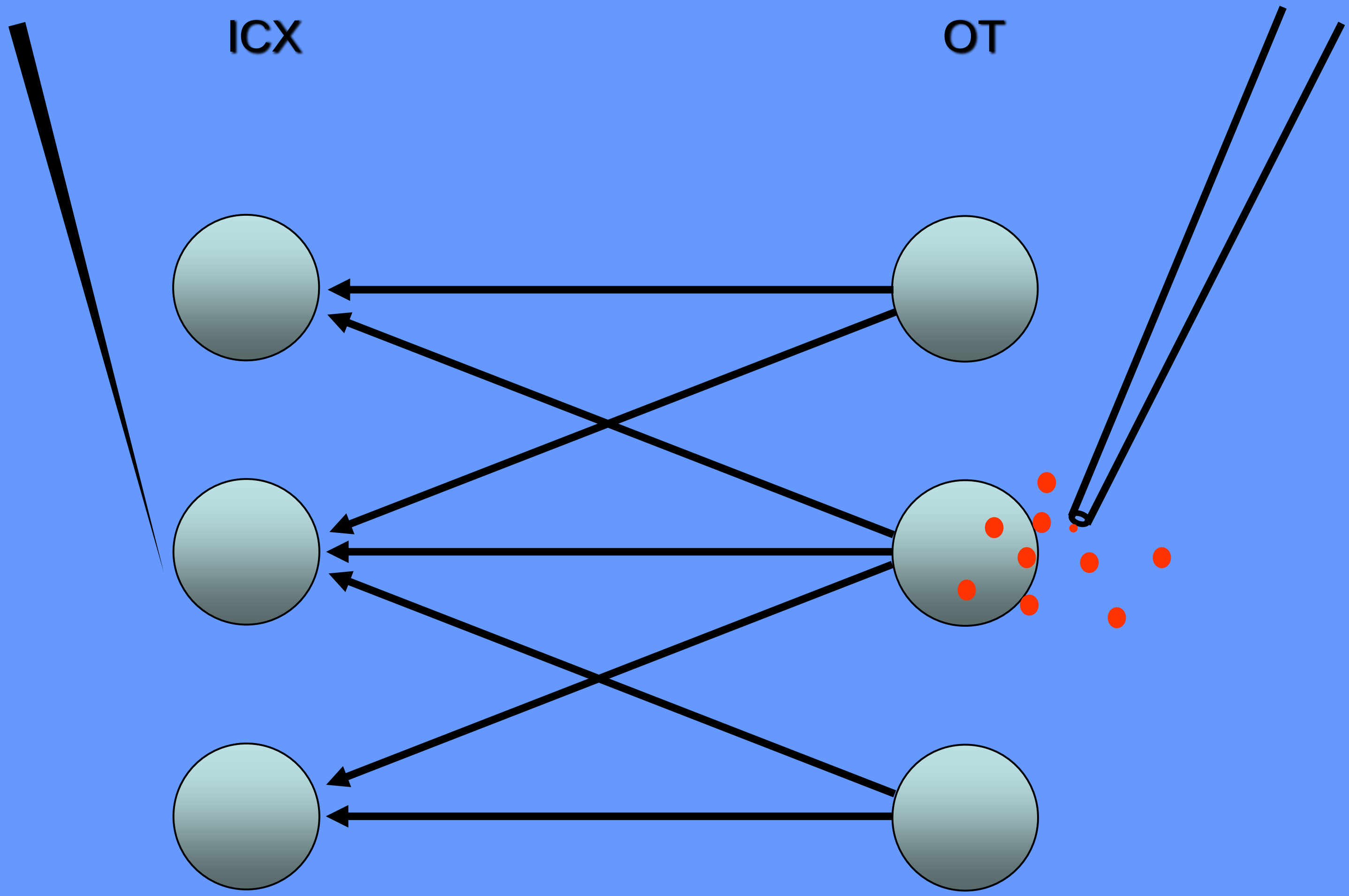

bicuculline
recording
iontophoresis barrels
recording barrel
ICC
ICX
500 µm
m
l
c
bic
c

Light responses in the ICX

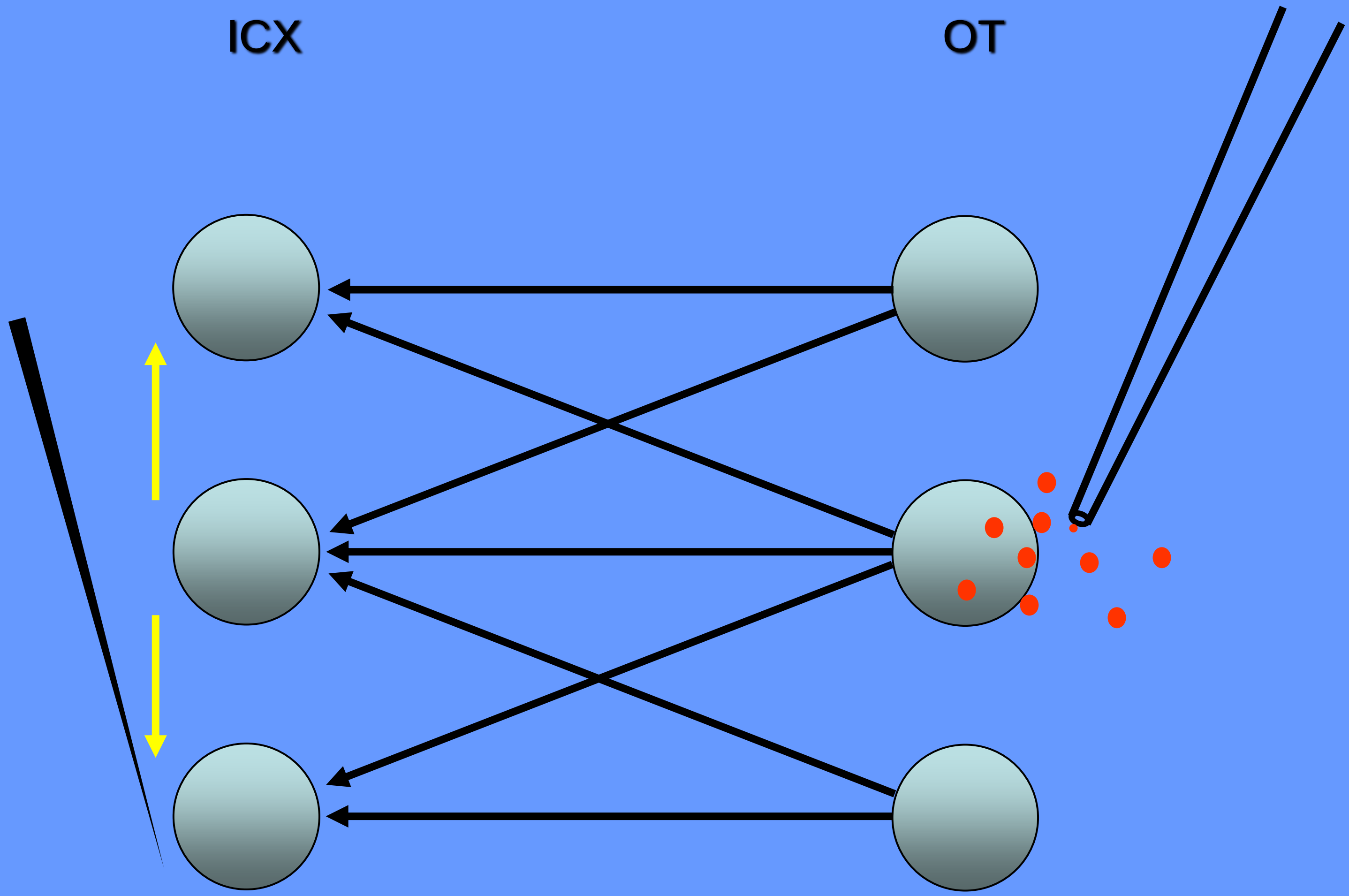


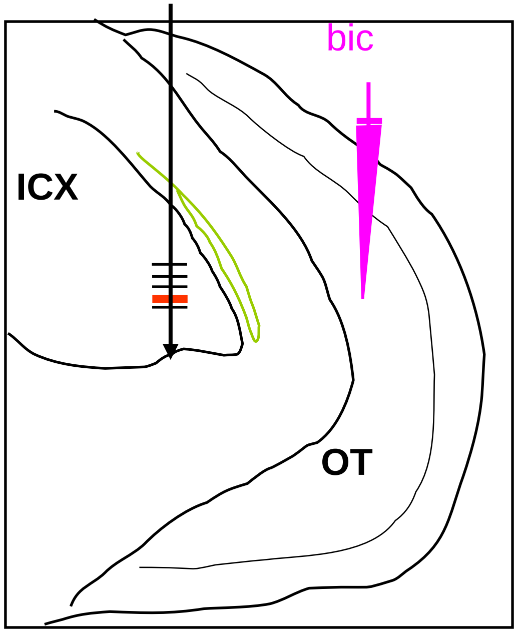
Visual Receptive Fields in the ICX



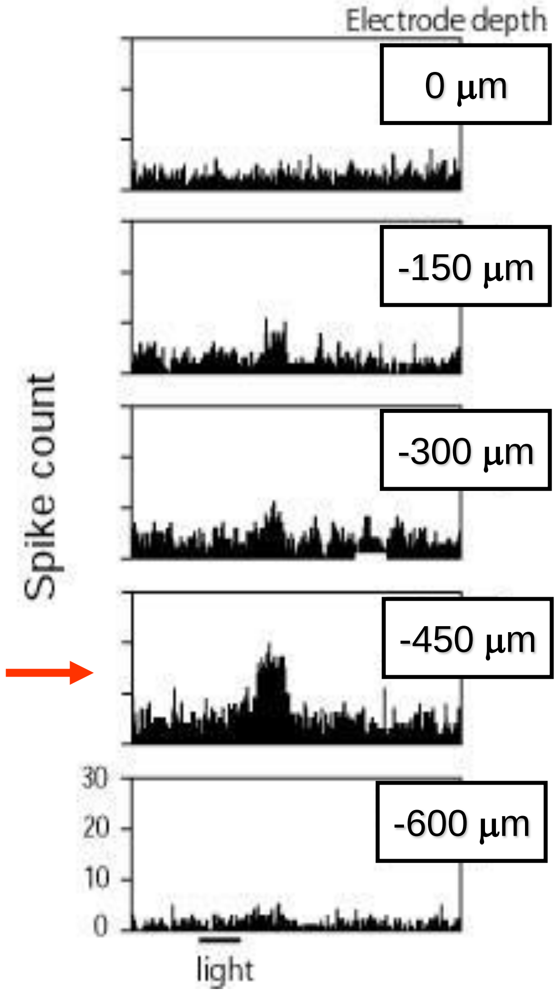


ICX
OT

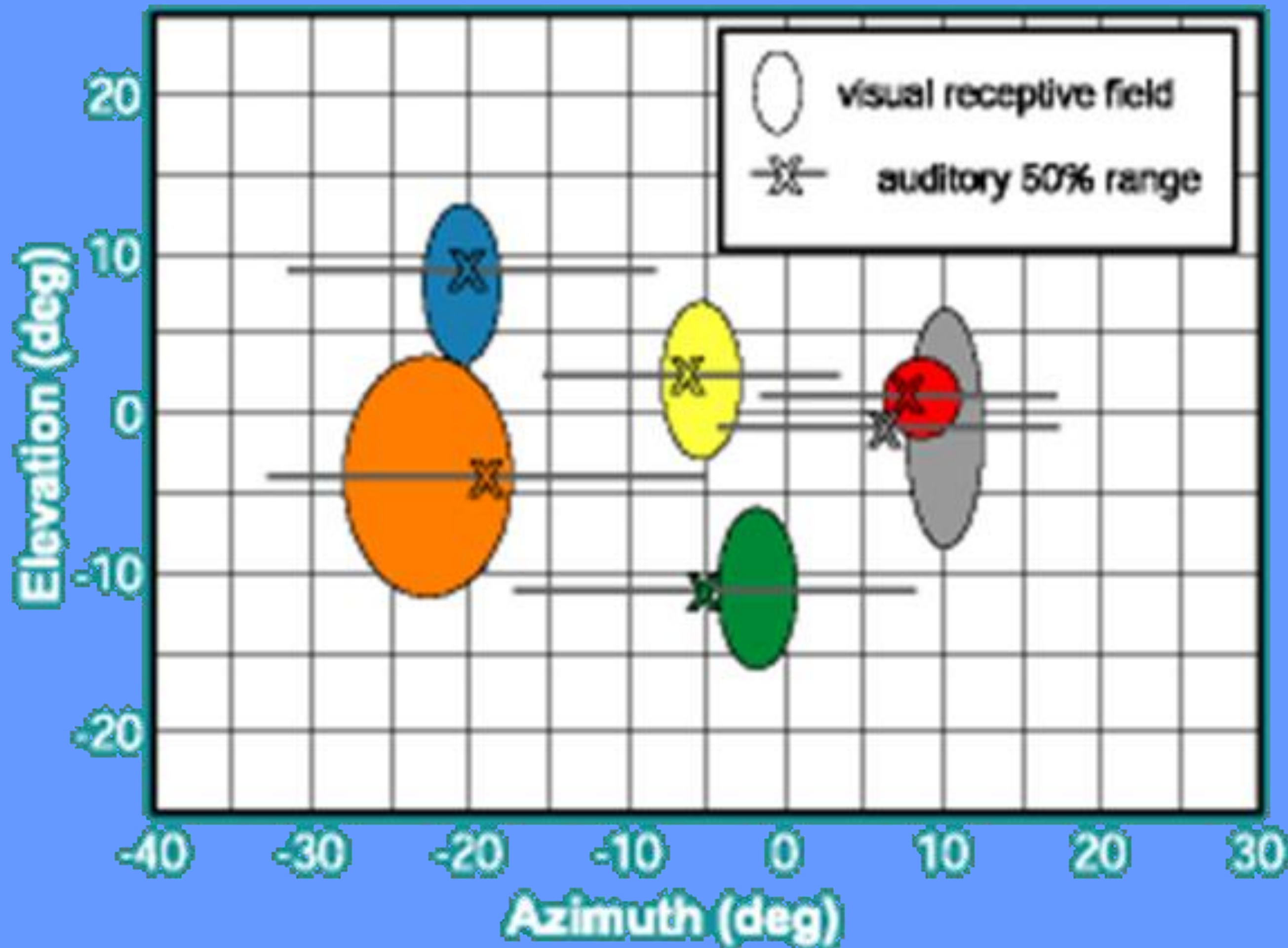

ICX
OT



bic
ICX
OT



Electrode depth
0 μm
-150 μm
-300 μm
-450 μm
-600 μm
Spike count
30
20
10
0
light


visual receptive field
auditory 50% range
20
10
0
-10
-20
Elevation (deg)
-40
-30
-20
-10
0
10
20
30
Azimuth (deg)

Properties of visual responses in ICX

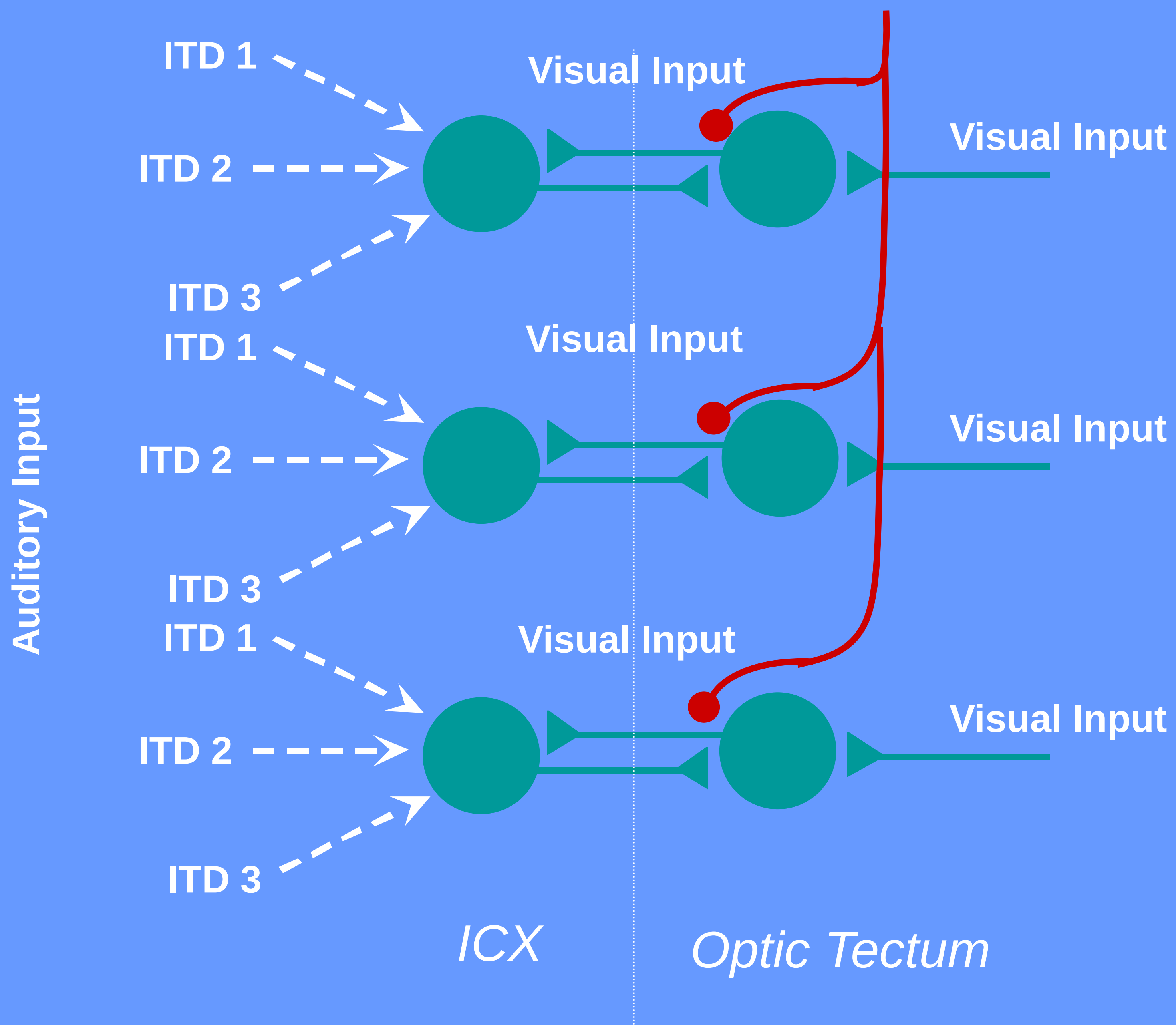
- Arrive from the OT

- Display spatially restricted visual receptive fields

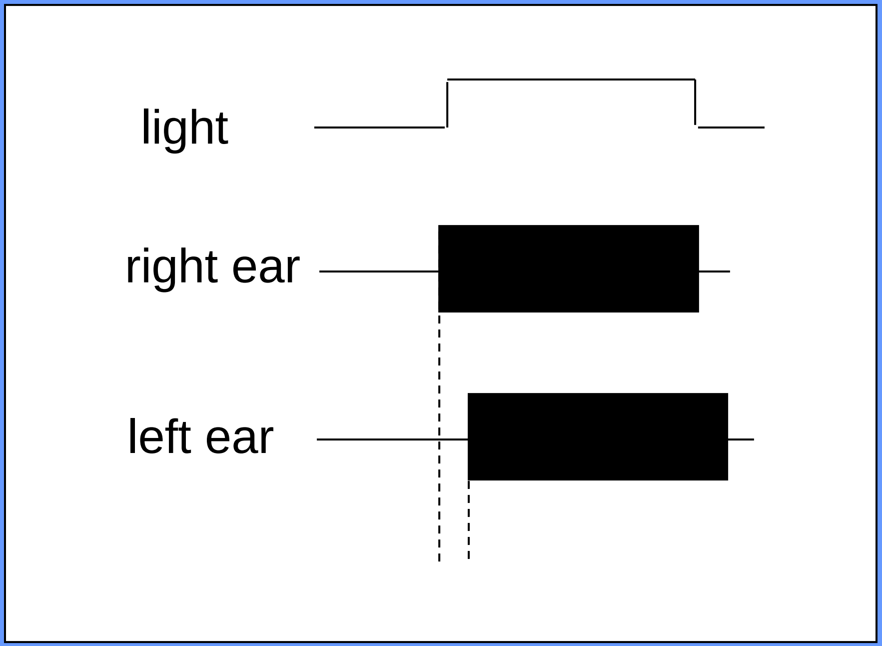
- Form a map of space

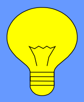
- Align with auditory spatial representation

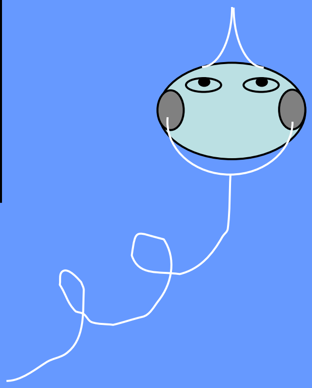
Model


gate
ITD 1
ITD 2
ITD 3
Visual Input
Visual Input
ITD 1
ITD 2
ITD 3
Visual Input
Visual Input
ITD 1
ITD 2
ITD 3
Visual Input
Visual Input
Auditory Input
ICX
Optic Tectum

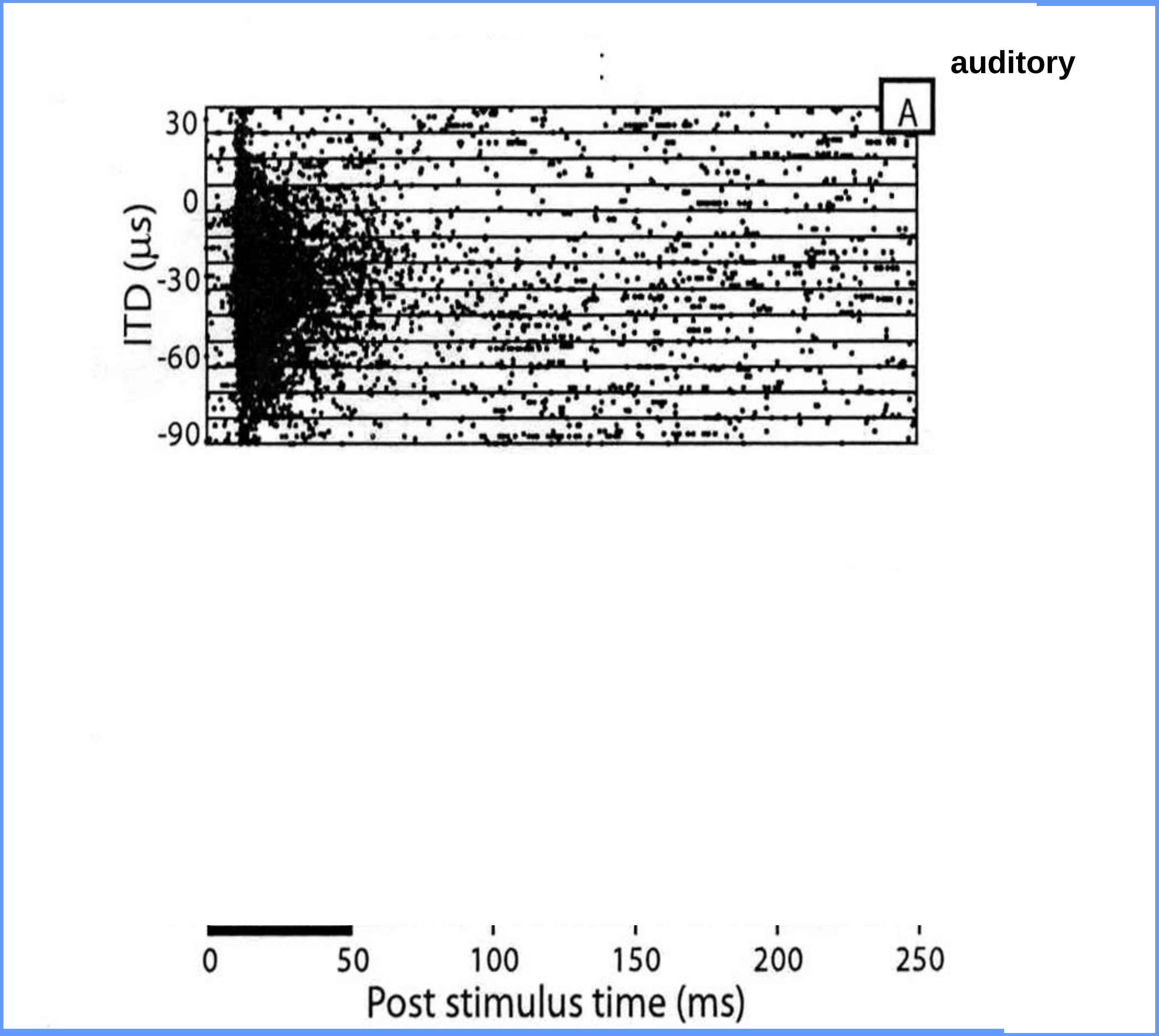
Bimodal Stimulus



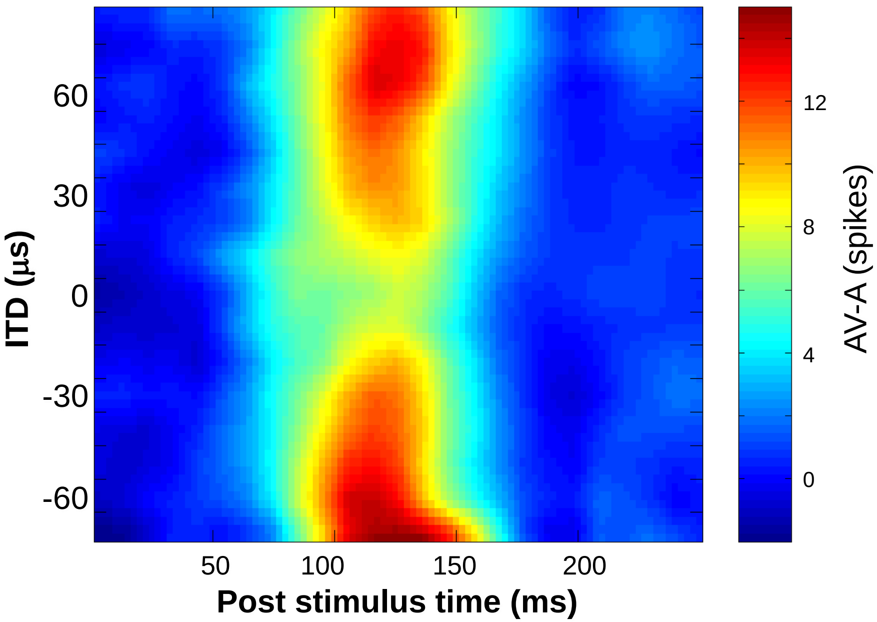


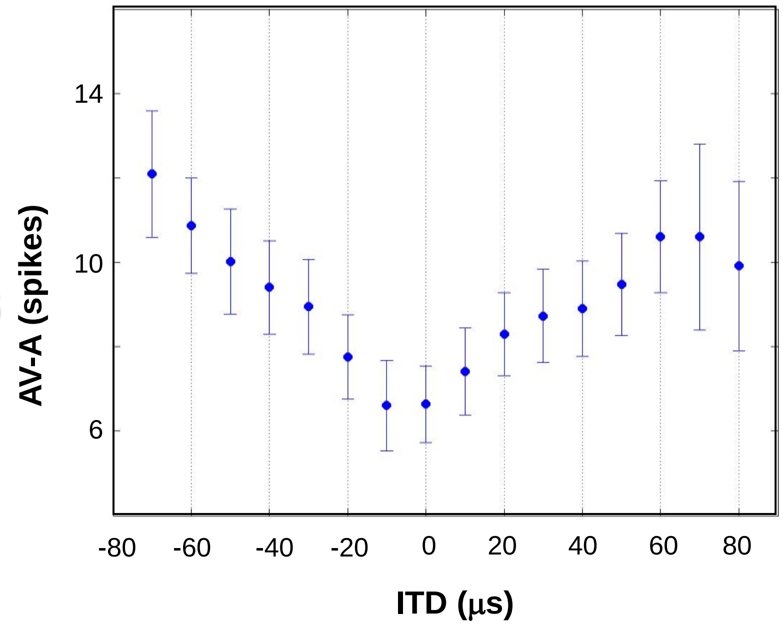


Visual and auditory interactions in the ICX



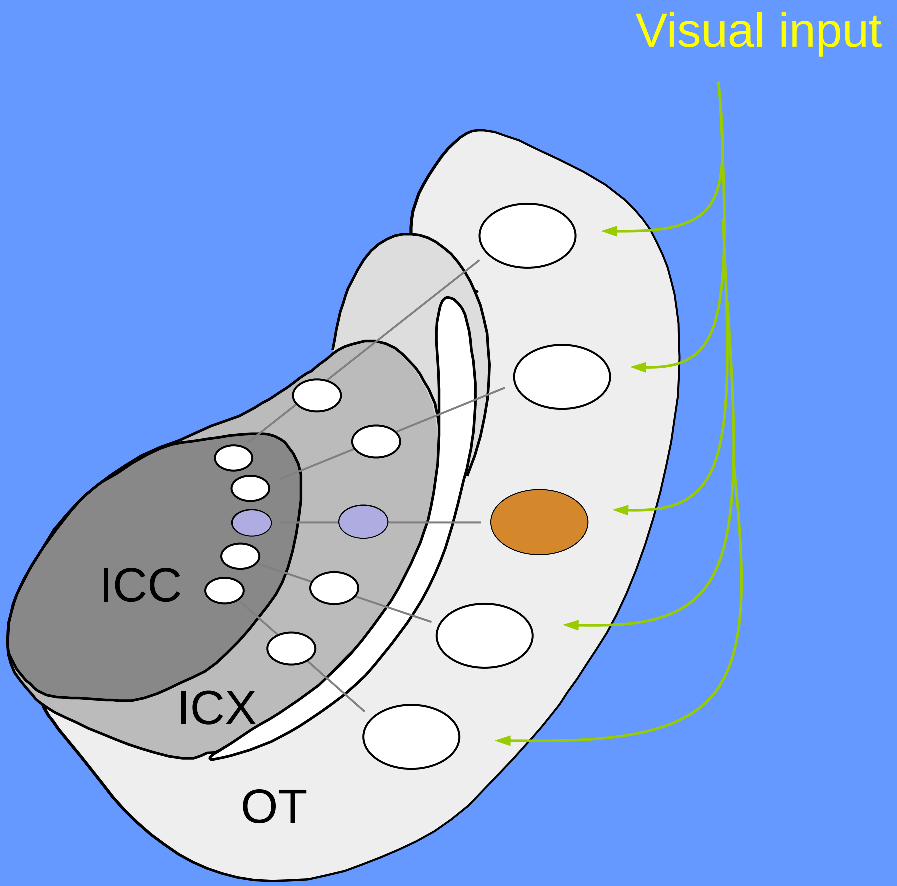
Average


60
30
0
-30
-60
ITD (µs)
50
100
150
200
Post stimulus time (ms)
12
8
4
0
AV-A (spikes)

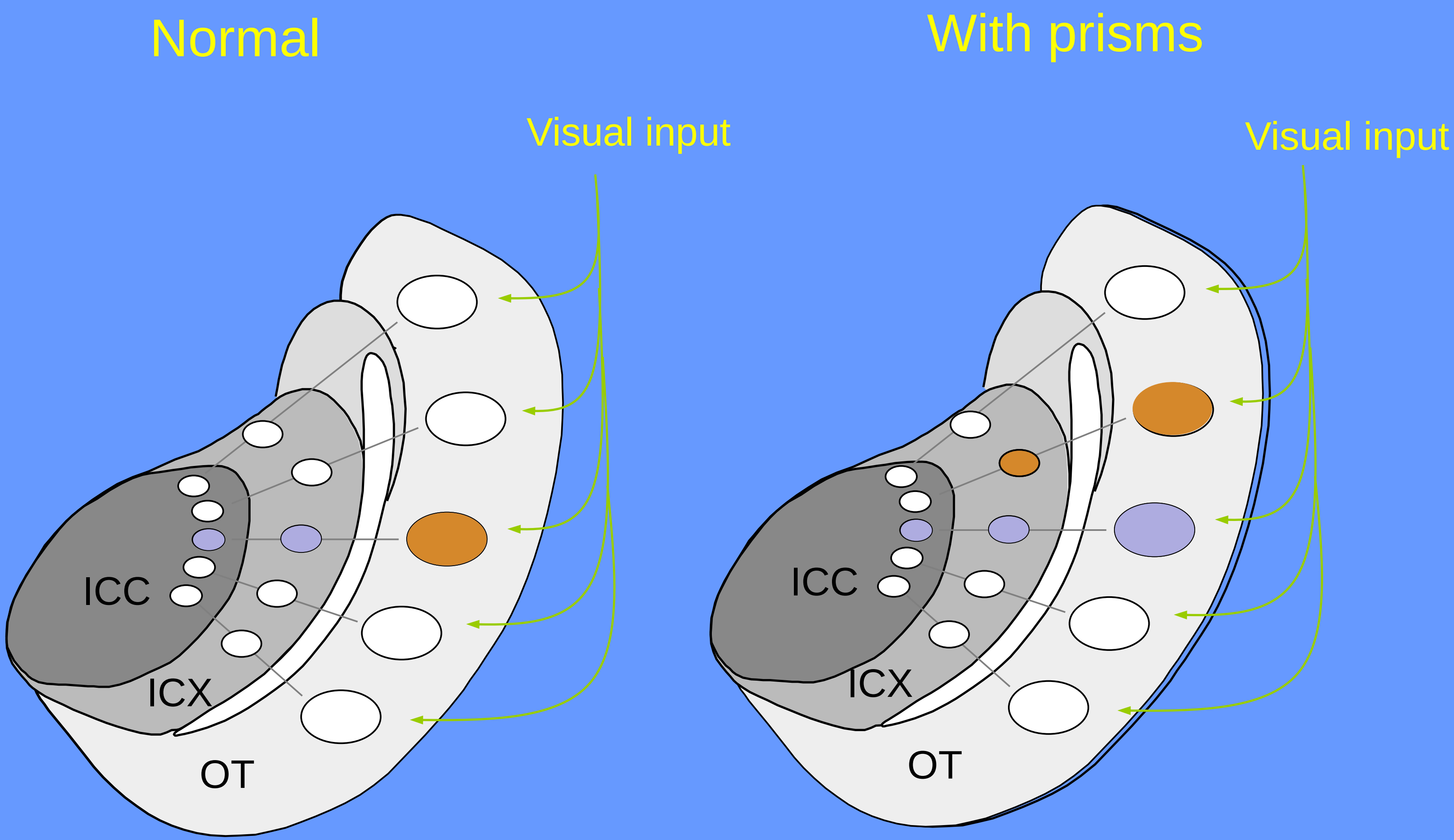

14
10
6
AV-A (spikes)
-80
-60
-40
-20
0
20
40
60
80
ITD (µs)

Bimodal stimulus

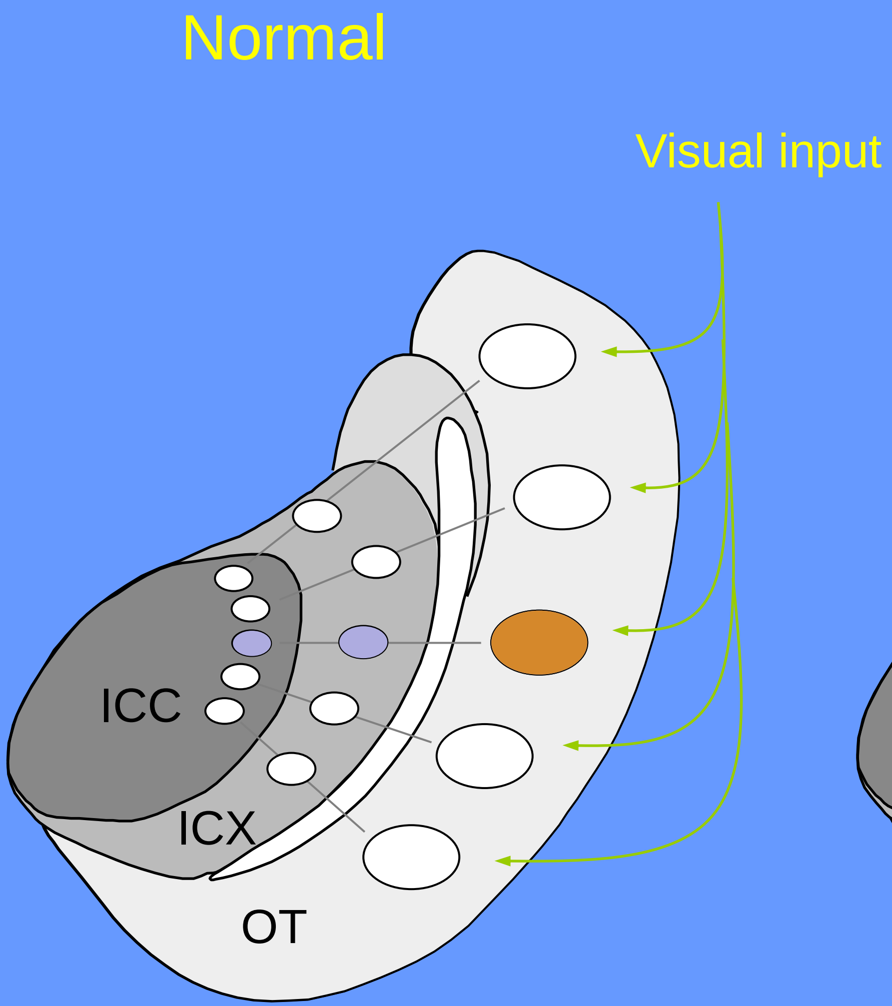
Normal

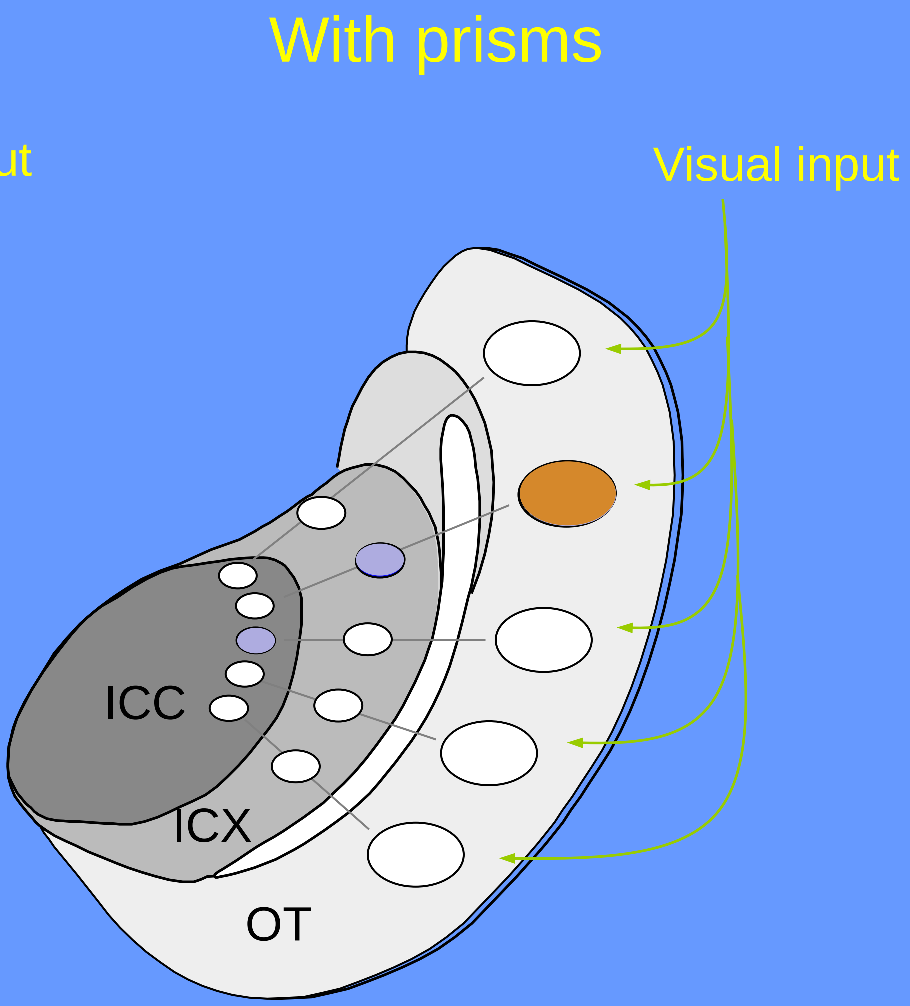


Bimodal stimulus



Bimodal stimulus





Summary

- An inhibitory gate controls the flow of visual information into the auditory system
- The visual signals are appropriate to serve as the instructive signal for auditory plasticity

Final Summary

- Studies in barn owls provided important insights on sound localization.

- Auditory map plasticity in barn owls is the first solved vertebrate example of experience-dependent plasticity.

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Shaked Ron
Mor Ben-Tov

Alon Wolf
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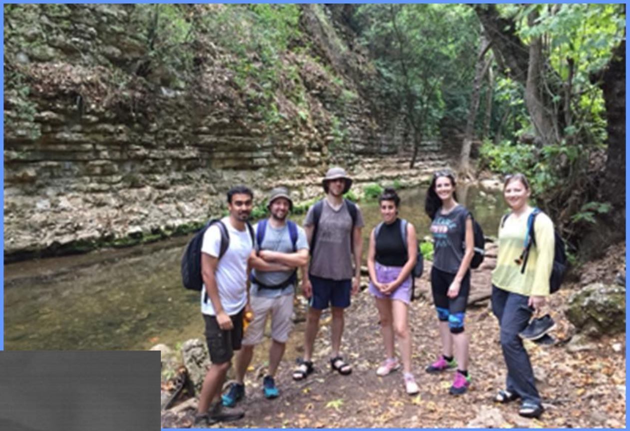
Nachum Ulanovsky
Dori Derdikman
Shai Berlin



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